COMPARATIVE FORAGING ECOLOGY OF TWO BROAD-RANGING MIGRANTS, GREY PLOVER *PLUVIALIS SQUATAROLA* AND WHIMBREL *NUMENIUS PHAEOPUS* (AVES: CHARADRII), IN TROPICAL AND TEMPERATE LATITUDES OF THE WESTERN INDIAN OCEAN

by

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Doctor of Philosophy

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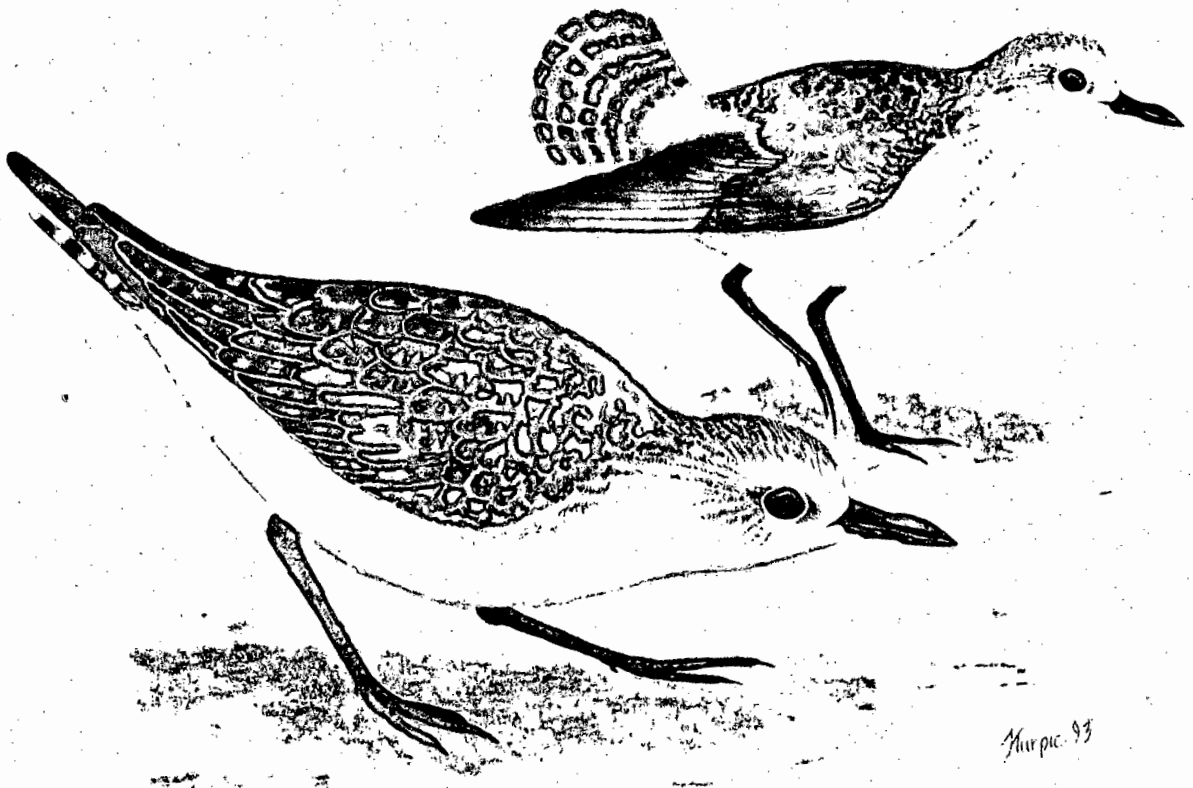

To my parents,
Derek and Janet Turpie

DECLARATION

This thesis reports the results of original research which I carried out under the auspices of the Percy FitzPatrick Institute of African Ornithology, University of Cape Town. All assistance that I received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Signed by candidate

Jane K. Turpie

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ABSTRACT. Turpie, J.K. 1994. *Comparative foraging ecology of two broad-ranging migrants, Grey Plover* Pluvialis squatarola *and Whimbrel* Numenius phaeopus *(Aves: Charadrii), at tropical and temperate latitudes of the western Indian Ocean.* Ph.D thesis, University of Cape Town.

A seasonal study of the nonbreeding foraging ecology of Grey Plovers and Whimbrels was undertaken at the Zwartkops estuary, South Africa, and additional data were collected from a variety of sites in tropical and south temperate latitudes during the premigratory period. The main objective of the study was to provide comparative data on shorebird foraging ecology in the southern hemisphere, in order to contribute to the general understanding of shorebird foraging behaviour and migration patterns.

Grey Plovers and Whimbrels are the commonest migrants on the Zwartkops estuary during the austral summer, and their numbers increase through the nonbreeding season to a peak during the premigratory period. Their distribution along the estuary in relation to prey biomass, and the seasonal patterns of energy intake rates and foraging effort in relation to bird densities and energy requirements suggest that strong intraspecific competition exists amongst both species. Nocturnal foraging occurred throughout the year. Foraging technique was altered at night, but net energy intake rates were not significantly different from those during the day.

Whimbrels at the Zwartkops estuary defended territories only during the spring arrival period, and cessation of defence was ascribed to increased pressure from conspecifics. Part of the Grey Plover population defended territories throughout the austral summer. Average territory size was inversely proportional to population size, and individual variation in territory size was related to resource abundance. A cost-benefit analysis suggested that the net benefit of territorial defence was equal for all territory holders. Nonterritorial Grey Plovers had a lower energy intake rate than territory holders, and this difference became more pronounced towards the end of the season.

Grey Plovers are visual foragers, using a stereotyped 'run-stop-search' foraging method, but the components of this behaviour altered according to different prey characteristics between sites. The versatile (visual/tactile) foraging method of Whimbrels allowed them to forage at higher densities than Grey Plovers, and to be more specialised in terms of prey choice.

Evidence suggested that access to resources was limited at most, if not all, the sites in this study, at least during the premigratory period.

Aggressive behaviour was highly variable between sites. Kleptoparasitic encounters occurred most frequently at sites where energy intake rates were low and where large prey species were eaten. The type and frequency of intraspecific encounters over foraging space were influenced by the density of conspecifics. Aggression rates over foraging space also were influenced by the spatial requirements for foraging on different prey types. Agonistic behaviour does not provide an adequate indicator of the overall effects of competition for inter-site comparison.

During the nonbreeding season, Grey Plovers and Whimbrels are more abundant in the northern than the southern hemisphere, but their densities frequently are higher at southern wetlands. Seasonal patterns of body mass are adapted to conditions at different latitudes, but risk of starvation is highest in north temperate areas. Energy intake rates are higher in the south, and survivorship in the south may be further enhanced by lower costs of thermoregulation and lower predation risks. Intraspecific competition played an important role in the foraging ecology of Grey Plovers and Whimbrels in south temperate and tropical, as well as in the northern hemisphere.

This study indicates that individuals migrating further south balance the costs of migration with higher survivorship on the nonbreeding grounds, and that competition for resources at these sites is no less intense than at sites closer to the breeding grounds. I thus propose that present-day migratory ranges are saturated.

ACKNOWLEDGEMENTS

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The historical view of avian community structure, that species adjust themselves in space in such a way as to result in the most complete use of resource production (MacArthur 1969) has regained popularity in recent years, but views have broadened to accept the fact that food limitation is not an all-or-none situation (Hutto 1990a). Before community structure can be adequately understood, it is neccessary to understand the factors that determine smaller-scale patterns, because community patterns have their source in individual behaviour (Wiens & Rotenberry 1981). Thus, a more reductionist approach to the study of ecological patterns is appropriate, by studying the foraging behaviour of individuals, while framing questions in the context of higher levels of biological organisation (Hutto 1990a). The study of avian community dynamics is further challenged by the complex life histories of migratory birds (Bennett 1980), and research is needed to clarify the role of food availability in regulating population size of migrants during the nonbreeding season (Terrill 1990). Whether competition affects bird distribution on a broad scale is the subject of much debate in terms of the explanation of migratory patterns (e.g. Greenberg 1986). Several studies provide evidence for strong competition for resources in the northern hemisphere, but comparable evidence from the southern hemisphere is lacking (Myers, Maron & Sallaberry 1985). There is thus a need for further investigation in order to elucidate the origin of long-distance migration

Shorebirds (suborder Charadrii) are one of the most migratory groups of birds, and undertake some of the longest migrations. Migrants encounter different food and foraging conditions on their breeding and nonbreeding grounds, and many shorebirds forage intertidally during the nonbreeding season. Inspired partly by the growing realization of the importance of the world's wetland habitats, and partly by their migratory habits, the interest in intertidally-foraging shorebird species has grown exponentially since the 1960's. Because of their tendency to forage gregariously in discrete wetland habitats, these are convenient species for study, at both the individual and community levels. Their essentially two-dimensional habitat simplifies the understanding of avian foraging ecology and the use of space.

In the development of the field of shorebird foraging ecology, the interactions between shorebird predators and their intertidal prey have received much attention in the literature (e.g. Wolff 1969, Goss-Custard 1970, Goss-Custard, Jones & Newberry 1977a, Pienkowski 1983, Zwarts & Wanink 1984, Kalejta 1991). Several processes relating to foraging behaviour have been recognised within shorebird populations. These include: (1) Energy intake rates of birds increase as prey densities increase (Goss-Custard 1977a,b); this advantage becomes less pronounced at high prey densities, due to the fact that the densities of birds themselves are correlated with the densities of their preferred prey, both within (Goss-Custard 1970, Bryant 1979) and

between wetlands (Goss-Custard, Kay & Blindell 1977b). (2) Increased bird densities result in increased interference between foraging birds (Goss-Custard 1980) and lead to the suppression of foraging activity (Zwarts 1981) and reduced prey intake rates (Goss-Custard 1976). (3) Aggression rates increase as bird densities increase (Burger, Hahn & Chase 1979, Goss-Custard 1977b, Vines 1980), but may be suppressed at very high densities (Recher & Recher 1969, Puttick 1981, Stawarczyk 1984). In some cases, shorebirds may circumvent the above problems by defending feeding territories (Myers, Connors & Pitelka 1979a).

The above findings indicate the important role intraspecific competition plays in the foraging behaviour and success of shorebirds, many of which have to satisfy their daily energy requirements within a tidally-limited period. Although the effects of competition on shorebird behaviour have been demonstrated in a variety of contexts, no measurable 'competition index' has been identified that might allow comparison of levels of intraspecific competition between different sites. The links between competition and agonistic behaviour, including territoriality, need to be clarified. The causes and consequences of territorial defence are poorly understood, particularly in terms of individual strategy (Myers 1984).

Two main problems have hindered the determination of how much difficulty shorebirds have in balancing their energy budgets. One is the difficulty of separating the amount of prey available to birds from measures of prey abundance (Myers, Williams & Pitelka 1980, Hutto 1990b), despite the fact that several factors are known to influence prey availability, such as temperature (Pienkowski 1981) and the activity of the birds themselves (Goss-Custard 1980). Secondly, very few studies have tackled the question of the relative foraging success of shorebirds at night (e.g. Zwarts & Dirksen 1990). The extent to which shorebirds forage at night has come to the attention of researchers only relatively recently (McNeil 1991), but the lack of information on the subject is due to the technical difficulties of accurate observation at night.

In addition, in order achieve a better understanding of avian behavioural ecology, the relationships between morphology and foraging behaviour, and between foraging behaviour and resource use, need to be investigated (Moermond 1990), as well as the mechanisms which underlie ecological plasticity (Greenberg 1990). Plovers (Charadriidae) and sandpipers (Scolopacidae) use different methods to find food, and this may have important repercussions on several aspects of their foraging ecology and distribution (Pienkowski 1979). Unlike sandpipers, plovers are restricted to foraging visually, and consequently face a different set of problems in acquiring food. The implications of foraging method to the diet, foraging behaviour and distribution of plovers and sandpipers needs to be investigated under a range of conditions.

Several shorebird species occupy broad latitudinal ranges during the nonbreeding season. Such species encounter conditions ranging from cold north temperate to warm tropical and south temperate parts of the world. Studies of the ecology of shorebirds under different conditions are essential to the understanding of their migration patterns (Evans 1976), and ultimately, to formulating strategies for their conservation (Terrill 1990). Most work on shorebirds has been carried out in the northern hemisphere, and several studies concentrate on how waders cope with severe weather conditions in these areas (e.g. Davidson 1981a,b). Comparatively few studies examine foraging ecology of shorebirds under more benign circumstances farther south. Consequently, inferences about long-distance migration have been made by the extrapolation of data from a limited range of latitudes (e.g. Pienkowski & Evans 1985). A primary objective of this study was to provide comparative information from tropical and, particularly, south temperate latitudes. Within this framework, the main aims of the study were:

1. To investigate the effects of different foraging methods on the diet, distribution and behaviour of shorebirds.
2. To determine seasonal patterns in the foraging behaviour and success of shorebirds at the south of their nonbreeding range, and the contribution of nocturnal foraging to their daily energy intake.
3. To investigate the link between competition and agonistic behaviour.
4. To determine whether competition influences shorebird foraging ecology in the southern hemisphere.
5. To examine latitudinal patterns in the ecology of migrants, in order to contribute to the understanding of intraspecific variation in migration distance.

These questions are addressed through a study of two shorebird species, Grey Plover *Pluvialis squatarola* and Whimbrel *Numenius phaeopus*. These species satisfy several important criteria for such a study. Grey Plovers and Whimbrels are representatives of the two largest shorebird families, the Charadriidae and Scolopacidae, respectively. The entire population of both species is migratory, and they are among the most cosmopolitan of intertidally foraging species, with nonbreeding ranges spanning over 100 degrees of latitude, and all the continental landmasses other than Antarctica (Hayman, Marchant & Prater 1986). Grey Plovers are one of the few cosmopolitan shorebird species which lack morphologically distinct subspecies (Cramp & Simmons 1983), thus facilitating intersite comparisons. Both species are among the largest representatives of their families. Large waders generally eat large prey (Baker & Baker 1973, Goss-Custard *et al.* 1977b), and this facilitates the accurate quantification of

energy intake rates.

The majority of work was carried out at the Zwartkops estuary, South Africa, where Grey Plovers and Whimbrels are the commonest Palearctic migrant species during the austral summer (Martin 1991). This estuary is one of the most important sites for shorebirds in the eastern Cape Province of South Africa (Underhill, Cooper & Waltner 1980), and one of the most important sites for Grey Plovers and Whimbrels in South Africa (Underhill & Cooper 1984). The Zwartkops estuary is particularly well suited to the study of shorebirds in South Africa because several studies have been made of its invertebrate populations and their behaviour (Els 1982, Hanekom 1980, Hanekom & Erasmus 1988, Hanekom, Baird & Erasmus 1988, Martin 1991).

Additional field work was carried out within tropical latitudes at Mida Creek, Kenya, at four sites in Mauritius, and at Tuléar, Madagascar, and in south temperate Africa, at the Breede and Berg River estuaries, western Cape Province, South Africa. The last site was the only one which falls outside of the western Indian Ocean.

Thesis layout

The first three chapters of this thesis concern the foraging ecology of Grey Plovers and Whimbrels at the Zwartkops estuary, South Africa. Chapter 1 describes seasonal changes in the foraging ecology of Whimbrels and Grey Plovers. Because many Grey Plovers are territorial at this site, this behaviour is dealt with separately in Chapter 2, which examines the seasonal dynamics of territoriality and individual solutions to the various costs and benefits involved in such behaviour. Chapter 3 is a comparative study of diurnal and nocturnal foraging by both Grey Plovers and Whimbrels, and investigates behavioural adaptations to nocturnal foraging as well as the energetic rewards.

Chapters 4 and 5 compare the foraging ecology and behaviour of Grey Plovers and Whimbrels at several tropical and south temperate sites at the same time of year. In Chapter 4, the geographic variations in foraging behaviour are compared for both species, and the consequences of these differences are discussed. Chapter 5 investigates the consequences of different foraging conditions for the nature and frequency of aggressive interactions amongst Grey Plovers and Whimbrels.

In Chapter 6, various aspects of the biology of Grey Plovers and Whimbrels are considered in a latitudinal context, synthesising the results from this study and drawing upon information available from the northern hemisphere. Latitudinal patterns are discussed in the light of hypotheses that have been put forward to explain intraspecific variation in migration distance.

SECTION I

SUMMARY

1. Numbers of Grey Plovers and Whimbrels at the Zwartkops estuary (104 ha) during this study ranged from 21 to 603 and 123 to 469 birds respectively. Grey Plover and Whimbrel density along the estuary was correlated with prey biomass. Grey Plovers defended fixed territories during the austral summer, and their densities on a 1.45 ha study area reached 10.3 birds.ha^{-1}. Whimbrel densities on the study area frequently exceeded 30 birds.ha^{-1}.

2. Juvenile Whimbrels foraged faster than adults, and achieved lower energy intake rates, but the difference in intake rates was not significant.

3. Whimbrel foraging behaviour and success varied over the low tide period, in relation to the availability of both prey and foraging space.

4. Grey Plovers and Whimbrels foraging during the daytime low tide period achieved their highest energy intake rates in the austral spring, decreasing through summer to a minimum during the premigratory period. Energy intake rates were correlated with conspecific density and mean nearest-neighbour distance, suggesting that interference plays an important role in regulating energy intake.

5. Grey Plover and Whimbrel foraging time per daytime low-tide period varied little throughout the year. Foraging time was limited by tidal exposure time, and conspecific densities. Throughout the year, Grey Plovers and Whimbrels foraged during the nocturnal low tide period, and Whimbrels also foraged in the saltmarshes when the mudflats were inundated.

6. Whimbrel aggression rates were related to foraging densities in different seasons, but much of the variation in this behaviour was attributable to social factors.

INTRODUCTION

The majority of migratory shorebirds (suborder Charadrii) forage intertidally on their nonbreeding grounds, where individuals must satisfy their daily energy requirements by obtaining sufficient food during a tidally limited foraging period. The difficulty experienced in satisfying these requirements depends on the balance between the birds' energy requirements and the amount of prey available per bird, both of which vary according to a number of abiotic and biotic factors (e.g. Evans 1976, Piersma 1987), and are difficult to measure. This balance is not only likely to determine the amount of competition in a population, but will manifest itself in two quantifiable elements: behaviour and energy intake rates. However, generalities about shorebird foraging ecology and competition during the nonbreeding season can only be formulated once the relationships between quantifiable factors are ascertained from a variety of populations and circumstances. Furthermore, in order to understand the selective pressures shaping the migration patterns of broad-ranging migrants such as Grey Plovers and Whimbrels, it is necessary to accumulate data on their foraging ecology from the extremes, as well as the core, of their ranges (Evans 1976).

This study investigates aspects of the foraging ecology of Grey Plovers and Whimbrels at the Zwartkops estuary, eastern Cape Province, South Africa, at the southern limit of their Afrotropical nonbreeding range. The aim of the study was to investigate distributional, energetic and behavioural evidence for competition, through analyses of bird distribution, behaviour and the dynamic interrelationships between energy intake rates, foraging behaviour and foraging densities, in the light of tentative estimations of prey availability and daily energy requirements. The following questions were addressed:

1. Does the temporal and spatial distribution of birds provide evidence for inter- or intraspecific competition among Grey Plovers and Whimbrels?
2. Do Grey Plovers and Whimbrels compete for the same prey?
3. How does age class and tidal state affect foraging behaviour and success?
3. How do energy intake rates vary seasonally, and what are the proximate causes of this variation?
4. Does foraging effort vary seasonally in relation to energy intake rates and energy requirements?
5. How much of the daily energy requirement is gained during the daytime low tide period, and does nocturnal foraging play an important role in satisfying this requirement?
6. Does aggressive behaviour provide evidence for intraspecific competition?
7. Why are the densities of Whimbrels unusually high at this site?

STUDY AREA

The Zwartkops estuary (33°52'S 25°38'E) experiences a warm temperate climate and has an intertidal mudflat area of 104 ha (Martin 1991), bordered by extensive *Spartina* saltmarsh habitat (Fig. 1.1). The main expanses of mudflats are located close to the river mouth and adjoin a network of creeks which dissect the saltmarsh areas. The mudflats are exposed for 3 - 5 hours in each tidal cycle.

Grey Plovers and Whimbrels are the commonest migrant shorebirds on the estuary. They prey predominantly on the thalassinid mudprawn, *Upogebia africana*, which accounts for 82% of the benthic invertebrate standing stock biomass and occurs at an average density of 218 (± 166 S.D.) per m^2 (Hanekom, Baird & Erasmus 1988). Although *Upogebia* size tends to decrease upstream, their density does not change significantly (Hanekom & Erasmus 1988, Martin 1991). A small proportion of these mudprawns moves onto the surface of the mud during the low tide period (probably due to parasite infestation), becoming readily available to visually-foraging birds. This behaviour is most pronounced among the larger size-classes of prawns (Martin 1991).

Grapsid crabs, *Cleistostoma edwardsii* and *C. algoense* are abundant, but because of their small average size (4-5 mm carapace width, Els 1982), they make up only 3% of the macrobenthic invertebrate biomass (Hanekom 1980). In addition, the saltmarshes support high densities of the crab *Sesarma catenata* (Els 1982). Grey Plovers also include a small proportion of polychaetes *Ceratonereis* spp. in their diet.

METHODS

The Zwartkops estuary was visited at approximately two monthly intervals between February 1990 and March 1991. Detailed observations were carried out on a small mudflat of 1.45ha (Fig. 1.1). Twenty-five unobtrusive coloured stakes were positioned at 20m intervals in a grid on the mudflat to facilitate distance estimates.

Numbers and distribution

The total number of Grey Plovers and Whimbrels on seven sections of the estuary was counted at low tide on seven occasions during the study period (Fig. 1.1). When possible, Grey Plovers were identified as adult or immature.

Energy requirements

Daily energy requirements were calculated from measurements of Grey Plovers and Whimbrels captured by mistnetting on the estuary. Lean mass was calculated from wing length (*W*) and field metabolic rate (FMR, $kJ.day^{-1}$) from body mass (*M*) as

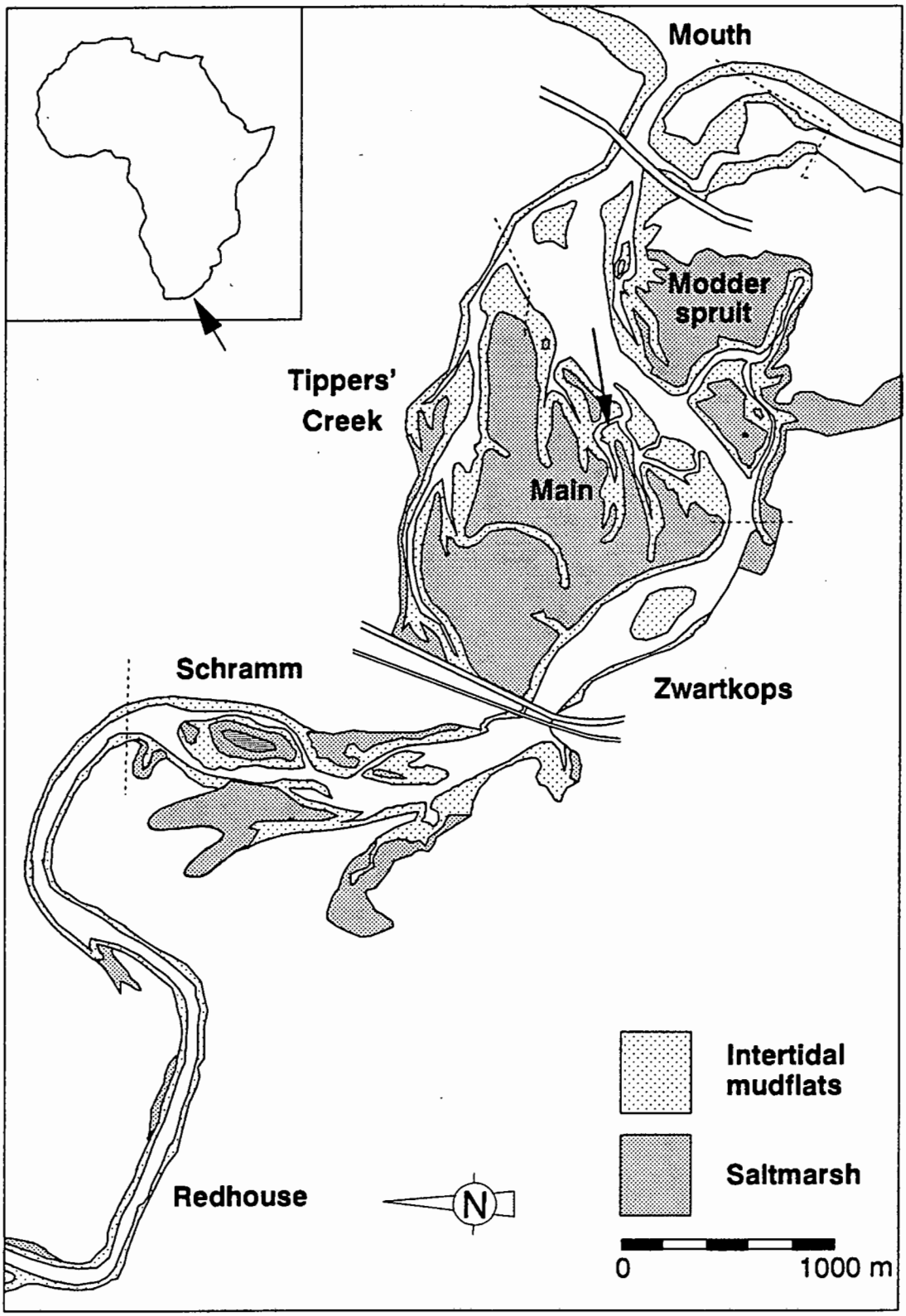


Figure 1.1. A map of the Zwartkops estuary, showing the seven counting sections separated by road bridges and dotted lines, and the position of the study area indicated by an arrow.

follows:

Grey Plover lean mass (g) = 1.124 x W (mm) - 39.42,
Whimbrel lean mass (g) = 2.96 x W (mm) - 328.65 (Zwarts *et al.* 1990c); and
FMR = 10.9 x M (g)$^{0.640}$ (Nagy 1987).

Prey availability

Els (1982) studied the seasonal abundance of *C. edwardsii* and *S. catenata* crabs at the Zwartkops estuary, and a seasonal study of the abundance and availability of *Upogebia africana*, was carried out by Martin (1991). Because most *Upogebia* are taken from the surface, prawn availability was estimated from the numbers emerging onto the surface per unit area per low tide period, on a monthly basis, at five sites (Martin 1991). In addition, during this study, surfacing prawns were systematically counted and removed from fifteen 400m^2 quadrats of varying prawn burrow density over one low tide period in March. In each plot the number of prawn burrow entrances was counted in at least five quadrats of 0.25m^2.

Foraging behaviour and energy intake

Grey Plovers and Whimbrels were observed, using binoculars and 15-60X telescopes, over each full daytime low tide period for approximately ten days during each visit. Observations were made over the spring tide period.

Instantaneous activity scans (Altmann 1974) were made at half-hourly intervals throughout each low tide period, during which the activity (foraging or resting) of each of the birds on the study area was recorded. Because aggression occurred whilst birds were foraging, birds involved in aggression were categorized as foraging. Resting birds included roosting, resting and preening birds. Transient groups of nonfeeding Whimbrels frequently visited the study area, particularly towards the end of the exposure period. In order to avoid inclusion of these birds in the calculations, the total population of the study area during each low tide period was taken to be the maximum number of birds foraging (F_{max}), and any total count exceeding F_{max} was reduced to this value. In the case of Grey Plovers, which were territorial during the summer, F_{max} was usually equal to the total number of birds on the study area. Thus average total time spent on the study area (1) and average time spent foraging (2) per low tide period were calculated as:

(1) Total time (min) = $\Sigma_{t(i..n)}\ [(Tt_i/F_{max}).I]$
(2) Foraging time (min) = $\Sigma_{t(i..n)}\ [(Ft_i/F_{max}).I]$

where Tt_i is the total number of birds at count t_i, Ft_i is the number of birds foraging at count t_i, F_{max} is the maximum number of birds foraging during the low tide period, and I is the count interval in minutes. In addition, instantaneous scans were carried out

during consecutive day and night low tide periods in March, July, August and December of 1991. Nocturnal observations were made using an HV7x200AT passive image intensifier (magnification 7x, light gain > 35 000x).

Daytime foraging behaviour and success were recorded during one-minute focal-animal observations of randomly selected foraging birds. The number of steps, prey capture attempts (pecks), and the number, type and size of prey taken was recorded. Distance (m) to the nearest foraging conspecific (nearest-neighbour distance) was estimated at 10 second intervals. A total of 1 572 and 2 149 minutes of focal observations were made of Grey Plovers and Whimbrels respectively. A detailed study of nocturnal foraging behaviour and success is presented in Chapter 3.

Crabs were too small to estimate their size accurately, so their average size was used. Prawn length (telson tip to rostrum tip) and polychaete length was estimated as a percentage of bill-length. Bill-length of Grey Plovers varies little between individuals; 31 birds captured at the Zwartkops estuary had a mean bill-length of 31.0 ± 1.2 (S.D.) mm (Martin 1991). Absolute bill-length variation in Whimbrels is greater. The mean bill-length of 26 Whimbrels at the Zwartkops estuary was 80.5 ± 5.4 mm. The distribution of bill-lengths was close to normal, with 73% of measurements falling within 1 S.D. (± 6.7%) of the mean. Because observations were directed at a random selection of birds, variation in bill-length is probably not a serious source of error in calculations of energy intake.

The accuracy of prawn size estimation was tested using stuffed birds and the same equipment and from the same distance as in the field. Bill-lengths of the stuffed birds were equal to the mean bill-lengths of the birds on the estuary. The following equations were used to calibrate field estimates (E_f in mm):
Grey Plover: actual length (mm) = 0.67 x E_f + 20.40 (n = 50, r = 0.88; Fig. 1.2a);
Whimbrel: actual length (mm) = 0.60 x E_f + 20.75 (n = 150, r = 0.82; Fig. 1.2b).

Prey biomass and energy content were calculated using the following equations: *Upogebia africana* dry mass (DM, in g) = 7.2×10^{-5} (carapace length mm)$^{3.152}$, energy content = 14.49 kJ.g^{-1}; *Cleistostoma* spp., mean DM = 0.054g, energy content = 14.86 kJ.g^{-1} (Martin 1991); *Ceratonereis* sp.: body length (mm) = 60.63 jaw length (mm) - 11.31, DM = 4.57×10^{-3} jaw length (mm)$^{2.79}$, energy content = 17.6 kJ.g^{-1} (Kalejta & Hockey 1991).

The observed gross energy intake was converted to net energy intake by correcting for assimilation efficiency. The assimilation efficiency of Whimbrels eating fiddler crabs is 65% (Zwarts & Blomert 1990). However, prawns have a lower proportion of inorganic material than crabs, and are probably digested with greater efficiency. Seabirds fed on krill have an average digestive efficiency of 71.4% (Jackson 1990) and waders feeding on mussel flesh have a digestive efficiency of

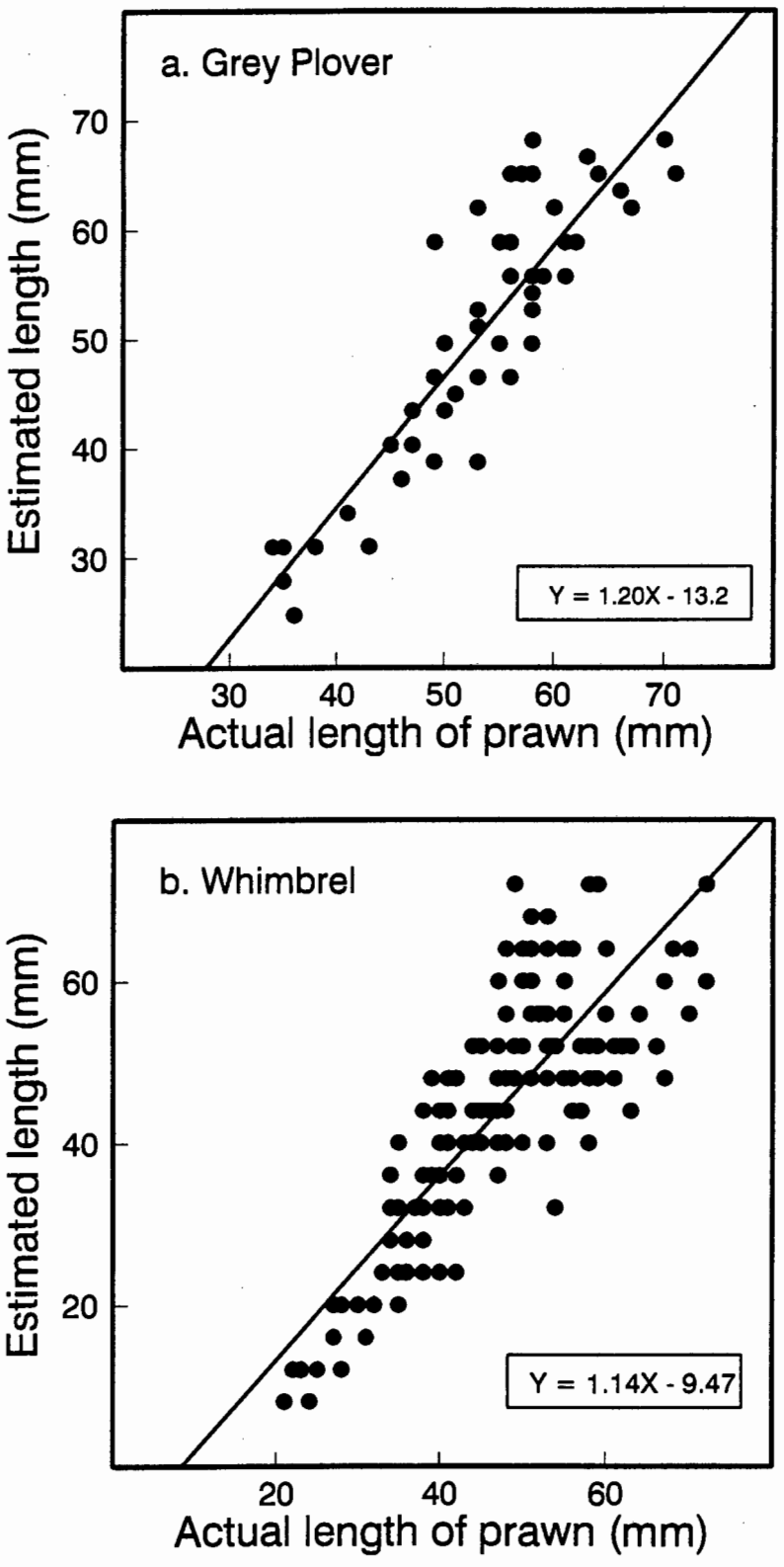


Figure 1.2. Correlation between estimated and actual lengths of *Upogebia* prawns held in the bill of a stuffed Grey Plover (a) and Whimbrel (b).

72.7% (Hockey 1984). An assimilation efficiency of 70% for prawns and 65% for crabs was assumed.

Both species also took very small prey items, identified only by the swallowing action of the birds. As these constituted a numerically small proportion of prey, they were ignored in calculations of energy intake rates.

Aggressive interactions were recorded during focal-animal observations, and in addition, one observer recorded all incidents of intraspecific aggression over the low tide period. Interactions were timed and were assigned to one of four categories (and numerical values) of intensity (after Recher & Recher 1969): threat (1); ground chase (2); air chase (3); and fight or territorial encounter (4).

RESULTS

Temporal and spatial distribution of birds

Peak numbers of Grey Plovers on the estuary during the study period were 603 and 470 birds in 1990 and 1991 respectively (Fig. 1.3a), and a maximum of 810 has been recorded previously. As many as 784 Whimbrels have been recorded on the estuary, but the seasonal peaks during the study period were 439 and 469 birds in 1990 and 1991 respectively (Fig. 1.3b). During the austral winter of 1990, 21 Grey Plovers and 123 Whimbrels remained on the estuary. Three of these Grey Plovers were adults in breeding plumage, of which one had a broken leg and another had a broken upper mandible.

Grey Plovers and Whimbrels regularly occupied all the intertidal areas of the estuary (Table 1.1), regardless of sediment type, except the sandy mouth area which is virtually devoid of prey animals (Hanekom *et al.* 1988). During the austral winter, the immature Grey Plovers congregated on the 'Main' mudflat area, but spread out to other areas as the number of adults increased during September (Table 1.1). No newly fledged juveniles had arrived by the end of September. The immature Whimbrels were more concentrated in the prawn-rich Modderspruit section during winter (July, Table 1.1). Densities of birds were consistently highest in the Main section, and the average summer densities (mid-September to March) of Grey Plovers and Whimbrels on each section of the estuary were positively correlated with the biomass of *Upogebia* (Martin 1991; Grey Plovers: $n = 7$, $r = 0.94$, $P < 0.01$; Whimbrels: $n = 7$, $r = 0.88$, $P<0.01$; Fig. 1.4). In addition, the richer sections of the estuary tended to fill up first (Fig. 1.5). The coefficient of variation (S.D./mean) of the proportion of the total population found in each section (excluding the Mouth section) was significantly lower in areas with high *Upogebia* biomass (Grey Plovers: $n = 6$, $r = -0.93$, $P< 0.01$; Whimbrels: $n = 6$, $r = -0.90$, $P< 0.05$).

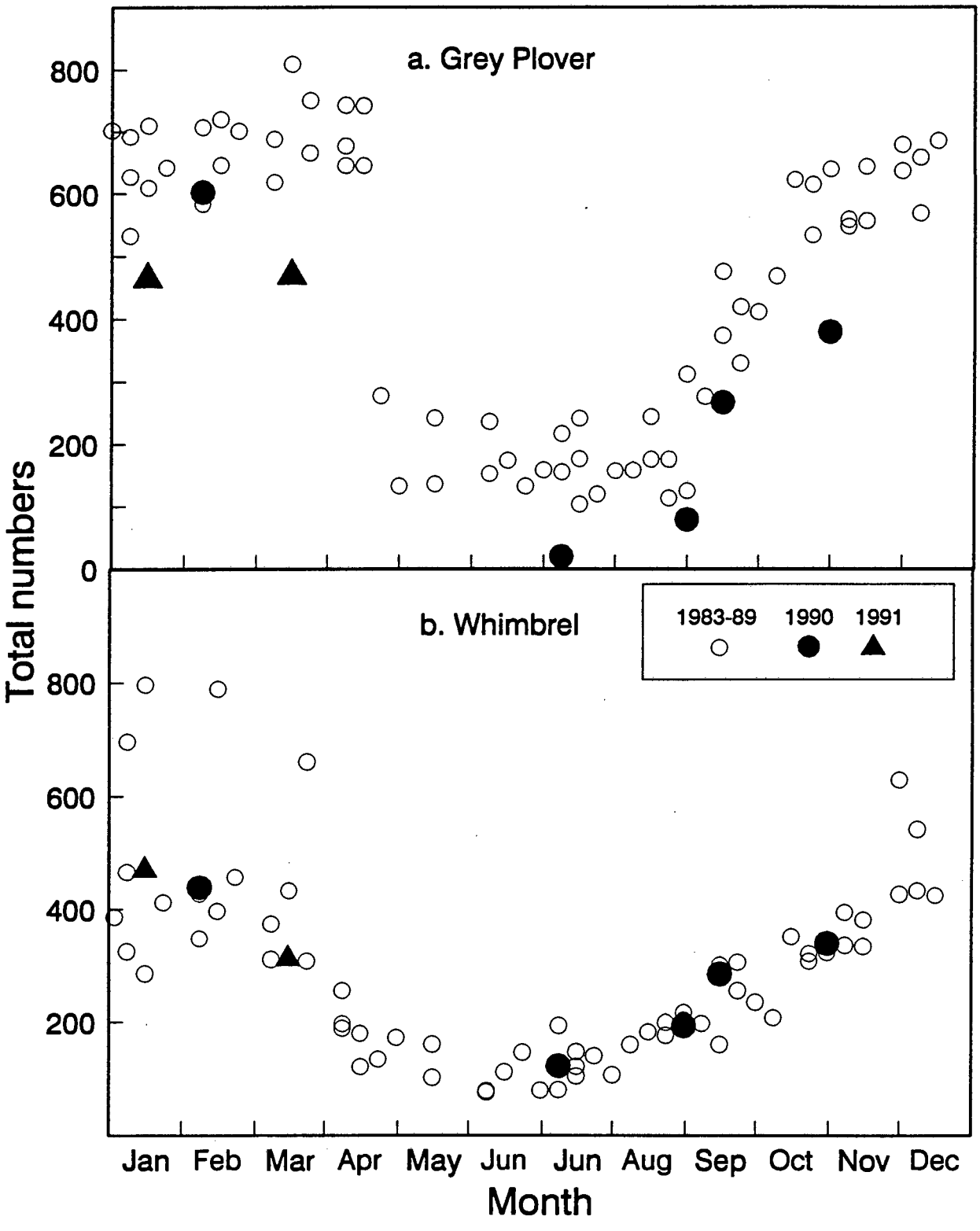


Figure 1.3. Numbers of (a) Grey Plovers and (b) Whimbrels counted in different months on the Zwartkops estuary during the study period (1990-1991) and during previous years by A.P. Martin (*in litt.*).

Table 1.1. Numbers and distribution of Grey Plovers and Whimbrels on the Zwartkops estuary from February 1990 to March 1991. Grey Plovers were separated by age class when possible, viz. adult (A) and juvenile (J). Sites are in order of increasing distance from the river mouth.

A: GREY PLOVERS

Site	Area (ha)	11 Feb	11 Jul		7 Sep		22 Sep		4 Nov	17 Jan	20 Mar
			A	J	A	J	A	J			
Mouth	11.8	-	-	-	-	-	-	-	-	-	-
Modder	18.6	117	-	-	4	1	28	4	69	82	82
Tippers	6.9	44	1	-	3	2	7	-	9	26	27
Main	24.4	199	2	18	30	14	136	9	169	157	171
Zwartkops	8.7	63	-	-	9	-	23	-	49	52	67
Schramm	19.0	141	-	-	16	-	56	5	86	139	135
Redhouse	14.9	39	-	-	-	1	-	-	-	9	-
TOTAL	104.3	603	3	18	62	18	250	18	382	465	470

B: WHIMBRELS

Site	Area (ha)	11 Feb	11 Jul	7 Sep	22 Sep	4 Nov	17 Jan	20 Mar
Mouth	11.8	-	7	-	-	-	-	-
Modder	18.6	80	47	33	57	67	93	76
Tippers	6.9	15	2	9	5	17	15	18
Main	24.4	210	38	79	162	162	208	133
Zwartkops	8.7	51	11	34	17	55	37	30
Schramm	19.0	45	10	39	44	29	81	50
Redhouse	14.9	38	8	11	-	9	35	9
TOTAL	104.3	439	123	205	285	339	469	316

Both Grey Plovers and Whimbrels were thus similarly distributed in time and space on the estuary, and there was no evidence of spatial segregation of the two species on a broad or local scale. Whimbrels and Grey Plovers were interspersed on the mudflats, Whimbrels foraging within the territories of Grey Plovers.

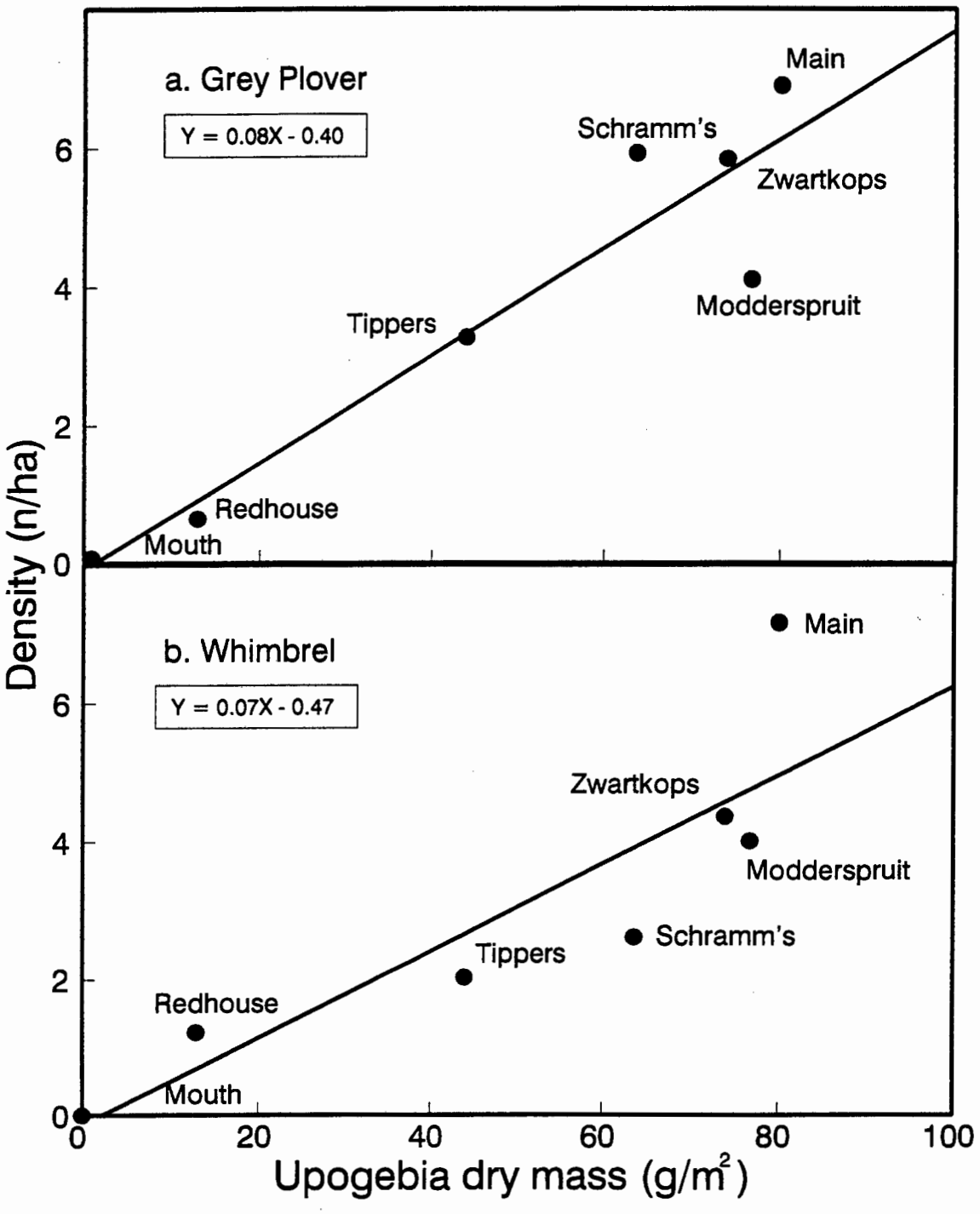


Figure 1.4. The relationship between (a) Grey Plover and (b) Whimbrel density on each of the seven sections of the estuary and dry mass ($g.m^{-2}$) of *Upogebia africana* measured in each section by Martin (1991).

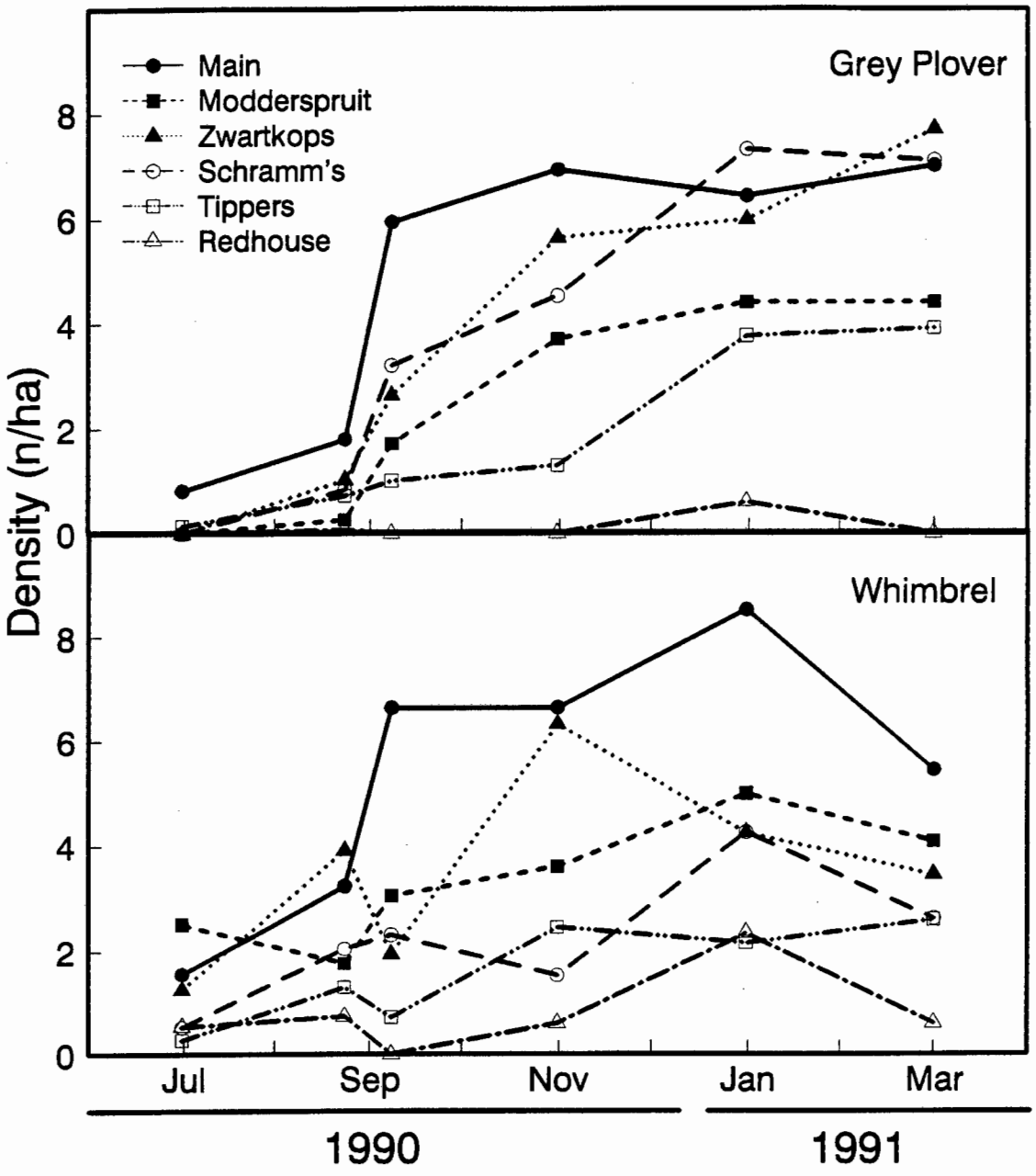


Figure 1.5. Changes in the densities of (a) Grey Plovers and (b) Whimbrels on different sections of the estuary from midwinter (July) to the end of summer (March).

Balancing the energy budget: requirements, resources and returns

Morphometrics and energy requirements

The average mass of seven juvenile Grey Plovers was 9% greater than lean mass calculated from wing length, but the mean measured mass of seven juvenile Whimbrels was almost identical to the their calculated lean mass (Table 1.2).

Lean mass could not be calculated for adults from October to January, as most of these birds were in the process of primary moult, and their outer primaries were not yet fully grown (a Whimbrel that was recaptured had wing measurements of 240 and 250 mm in December and March respectively). Adult Whimbrel lean mass calculated from wing length in March (414 g; Table 1.2) was similar to the average mass of Whimbrels captured in November (416 g), prior to the onset of premigratory fattening. Lean mass calculated for adult Grey Plovers was between 189 g and 198 g in the months when birds were not undergoing primary moult, but was lower than the mass of adults in September (210 g; Table 1.2). There is a possibility, therefore, that the equation for lean mass developed for Grey Plovers in West Africa (Zwarts *et al.* 1990c) does not accurately predict the lean mass of Grey Plovers in South Africa. Grey Plover juvenile and adult lean masses were thus taken to be 200 and 210 g respectively (Table 1.2). In December, Whimbrels weighed considerably less than their calculated lean mass, but this was possibly related to the fact that they were all in active moult. The daily net energy requirements of adults prior to the fattening period (September - December) were calculated from the average lean mass of adults, as 334 $kJ.d^{-1}$ for Grey Plovers and 516 $kJ.d^{-1}$ for Whimbrels (Nagy 1987).

Although as much as a 30% increase in mass has little effect on basal metabolic rate (Kersten & Piersma 1987), true energy requirements of the Whimbrels during the premigratory period (February - March) were probably greater than predicted by lean mass, as Nagy's (1987) equation does not account for the extra energy required to lay down these premigratory stores. It was calculated that Grey Plovers and Whimbrels at the Zwartkops increase in mass during the premigratory period at rates of approximately 2.3 and 4.5 $g.day^{-1}$ respectively (1.1% of lean mass, Zwarts & Dirksen 1990). Although the ratio of protein and fat comprising these stores is still disputed (see Lindstrom & Piersma 1993), evidence suggests that the protein component is greater in larger species. However, there may also be an increase in the fat component in birds which migrate a longer distance (Zwarts *et al.* 1990c). An estimated 33-36% of the premigratory mass increase of Bartailed Godwits (*ca.* 220g lean mass) in West Africa comprises protein (Lindstrom & Piersma 1993). I made a conservative estimate of the ratio of protein to fat deposition of Grey Plovers and Whimbrels in South Africa

Table 1.2. Mean mass and wing lengths (± S.D.) of Grey Plovers and Whimbrels caught at the Zwartkops estuary from September to April, during this study and by A.P. Martin (*in litt.*). Lean mass is calculated from wing length (Zwarts et al. 1990c), and FMR is calculated from Nagy's (1987) equation, both for measured and lean mass. Whimbrel measurements include those of two birds recaptured in different months.

Age class	Month	n	Measured mass (g)	DEE (kJ)	Wing length (mm)	Lean mass (g)	DEE (kJ)
GREY PLOVER							
Juv	All	7	200 (38)	324	198 (6)	183	306
Adult	Sep	2	210 (8)	334	211 (4)	198	322
	Oct	2	242 (3)	366	200 (1)		
	Nov	6	214 (15)	338	203 (4)		
	Dec	2	230 (2)	353	203 (3)		
	Jan	1	218	342	201		
	Mar	4	253 (22)	376	204 (9)	190	313
	Apr	3	312 (16)	430	203 (3)	189	312
WHIMBREL							
Juv	All	7	362 (25)	473	233 (9)	361	472
Adult	Nov	3	416 (38)	517	246 (10)		
	Dec	6	384 (40)	491	233 (8)		
	Jan	1	467	557	246		
	Feb	1	530	604	255		
	Mar	11	580 (36)	640	251 (6)	414	516

as 30:70, thus possibly over- rather than underestimating their premigratory energy requirement: if the energy content of fat and protein (including water) is 38.9 and 5.8 $kJ.g^{-1}$ respectively (Whittow 1986 in Zwarts & Dirksen 1990), the extra net energy required for these depositions would be 29 $kJ.g^{-1}$, raising the FMR of adults from 334 to 401 $kJ.day^{-1}$ for Grey Plovers and from 516 to 646 $kJ.day^{-1}$ for Whimbrels.

Premigratory fattening probably commences during January, and the average energy requirements of adults during January were estimated to be intermediate between early summer and premigratory values.

Foraging methods and diet

Grey Plovers foraged visually, in a run-stop-search manner, whereby the bird stopped to search for prey before moving to capture an item or to search from a new position. This behaviour did not change whether the birds were searching on mud or in water. Whimbrels, on the other hand, walked continuously whilst foraging, and foraged predominantly visually, both on mud and in water, although tactile foraging was employed occasionally.

Both species consumed large *Upogebia* mudprawns and small *Cleistostoma* crabs on the study area, and Grey Plovers also took small polychaetes. Differences in dietary composition are analysed in further detail in Chapter 4. On average, mudprawns accounted for 89.0% (± 11.0% S.D., n = 8 mo) and 88.5% (± 3.7%, n = 8 mo) of net energy consumption of Grey Plovers and Whimbrels, respectively. There was no significant difference in the size distribution of prawns taken by Grey Plovers and Whimbrels (X^2_5 = 17.8; Fig. 1.6), but Grey Plovers took longer than Whimbrels to handle prawns of equivalent size (Fig. 1.6).

The effect of age on foraging efficiency

The numbers of juvenile Grey Plovers were too low during this study to allow adequate comparison of their foraging behaviour with adults at the same time of year.

Juvenile Whimbrels walked significantly faster than adults and attempted prey capture significantly more frequently than adults (Table 1.3). Although the rates of prey capture and energy intake recorded were lower for juveniles, these differences were not significant. Similarly, the higher aggression rate of juveniles was not significantly different from adults, but this may be due to the small sample size. There were no significant differences in the average intensity of encounters or average nearest neighbour distances between adults and juveniles (Table 1.3).

Tidal effects on foraging behaviour and success

Unlike Grey Plovers, which remained on fixed territories, and thus at constant densities

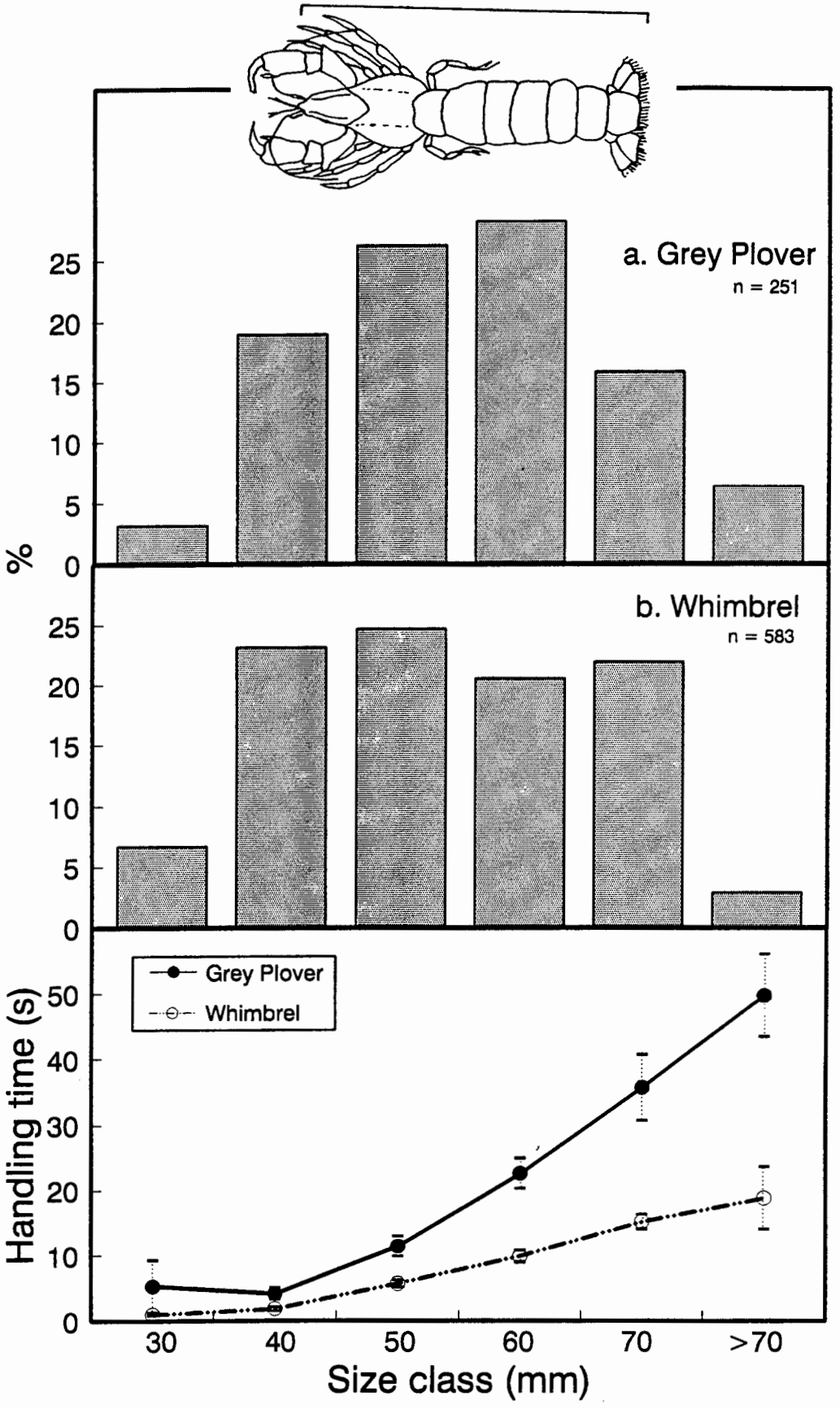


Figure 1.6. Percentage frequency of prawns of different size classes in the diets of (a) Grey Plovers and (b) Whimbrels, and the mean (± S.E.) handling time (s) for prawns in each size class by each species.

Table 1.3. Average (± S.D.) numbers of steps, pecks and prey captured, net energy intake ($kJ.min^{-1}$), number of aggressive encounters per minute, encounter intensity and nearest-neighbour distance (NN) for adult and juvenile Whimbrels during March 1991.

Age	*n*	Steps. min^{-1}	Pecks. min^{-1}	Prey captured.min^{-1} Crabs	Prawns	Total#	Net energy intake	Aggression $n.min^{-1}$	intensity	NN (m)
Adult	294	92 (38)	6.4 (4.5)	0.30	0.27	0.65	1.62	0.065	2.21	18.5 (16.8)
		***	***	n.s.	n.s.	n.s.	n.s	n.s.	n.s.	n.s.
Juv	80	126 (43)	10.2 (5.4)	0.21	0.25	0.60	1.14	0.113	2.44	18.0 (15.3)

*** $P < 0.001$, n.s. = not significant; steps, pecks and aggression intensity: Student's t-test; all others: sampled randomisation test.
#Includes unidentified prey items.

throughout the low tide period, Whimbrel numbers changed substantially over the exposure period (Fig. 1.7). Aspects of Whimbrel foraging behaviour and success were therefore analysed in relation to the stage of low tide.

Whimbrels occupied the mudflat throughout the exposure period, some birds arriving when the study area was still covered by a few centimetres of water, and a few often remaining for a short period after the mudbank was inundated. The study area took one to two hours to become fully exposed, and less than an hour to flood. The number of Whimbrels present on the study area was highest during the middle of the exposure period (Fig. 1.7). At the beginning and end of the exposure period, temporary roosting flocks of Whimbrels gathered in nearby creeks. Whimbrels also foraged at mid-tide levels in the saltmarshes, but at high tide these areas were flooded.

Hourly data from all but the winter months were combined to show the effects of tidal state on various aspects of foraging (Fig. 1.8). Nearest neighbour distances did not vary much over the low tide period, but were slightly smaller at the beginning and end of the exposure period, when birds concentrated their foraging along the water's edge (Fig. 1.8a). Foraging effort (steps and pecks combined) was also fairly constant, but decreased towards the end of the low tide, this being partly due to the birds' foraging more slowly in water on the incoming tide. Energy intake rates were high as the tide first receded, and relatively constant thereafter.

The average rates of intake of both crabs and prawns by Whimbrels were highest at the beginning and end of the low tide period (Fig. 1.8b). The total number of prawns consumed on the study area per hour closely follows the tidal pattern of prawn emergence found by Martin 1991 (Fig. 1.9). Although the tidal patterns of crab availability are unknown, the crab consumption rate was included in Fig. 1.9 for comparison.

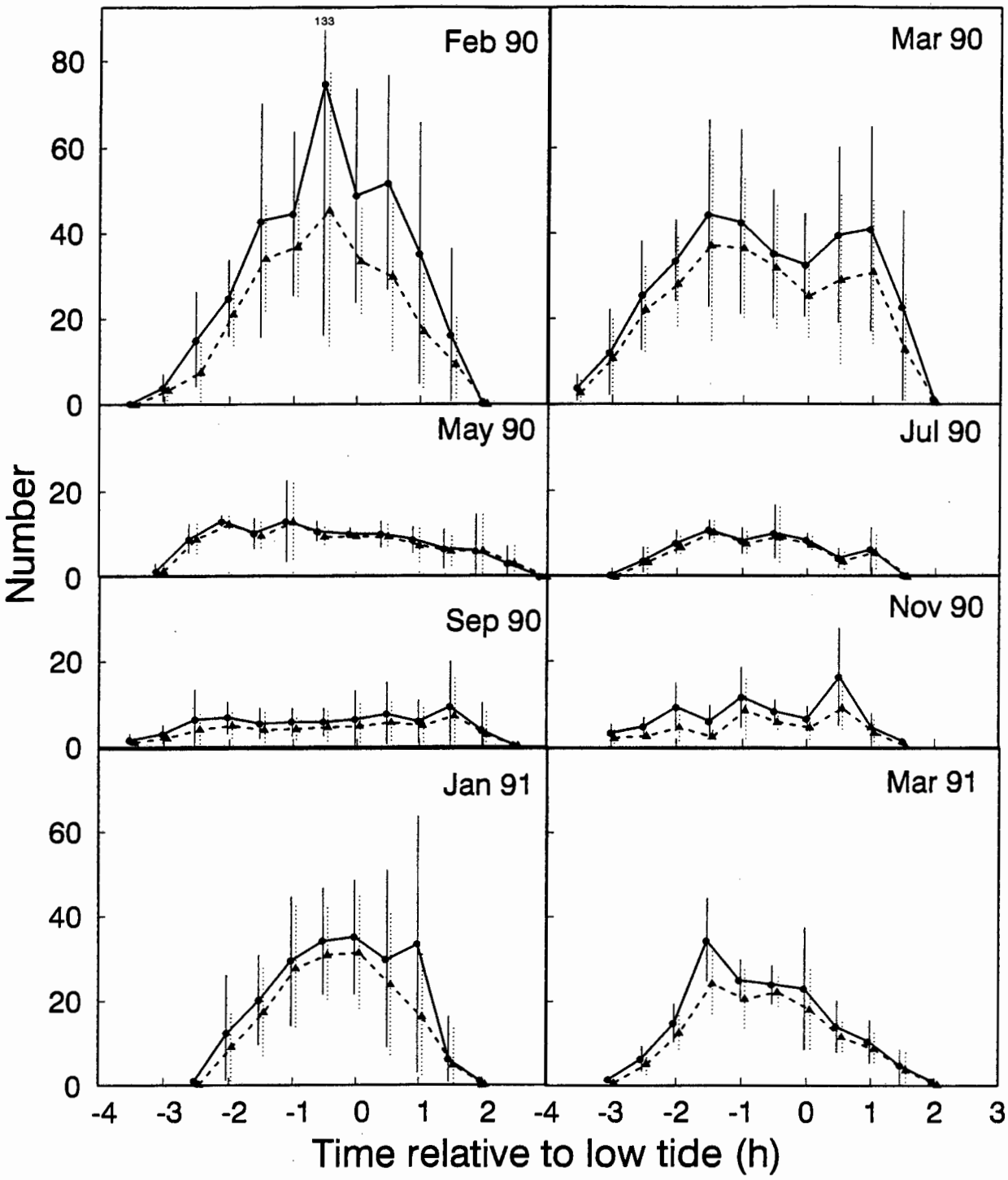


Figure 1.7. The mean number of Whimbrels foraging (dotted line) and their mean total numbers on the study area (1.45 ha) per half-hour over the daytime low tide period in different months.

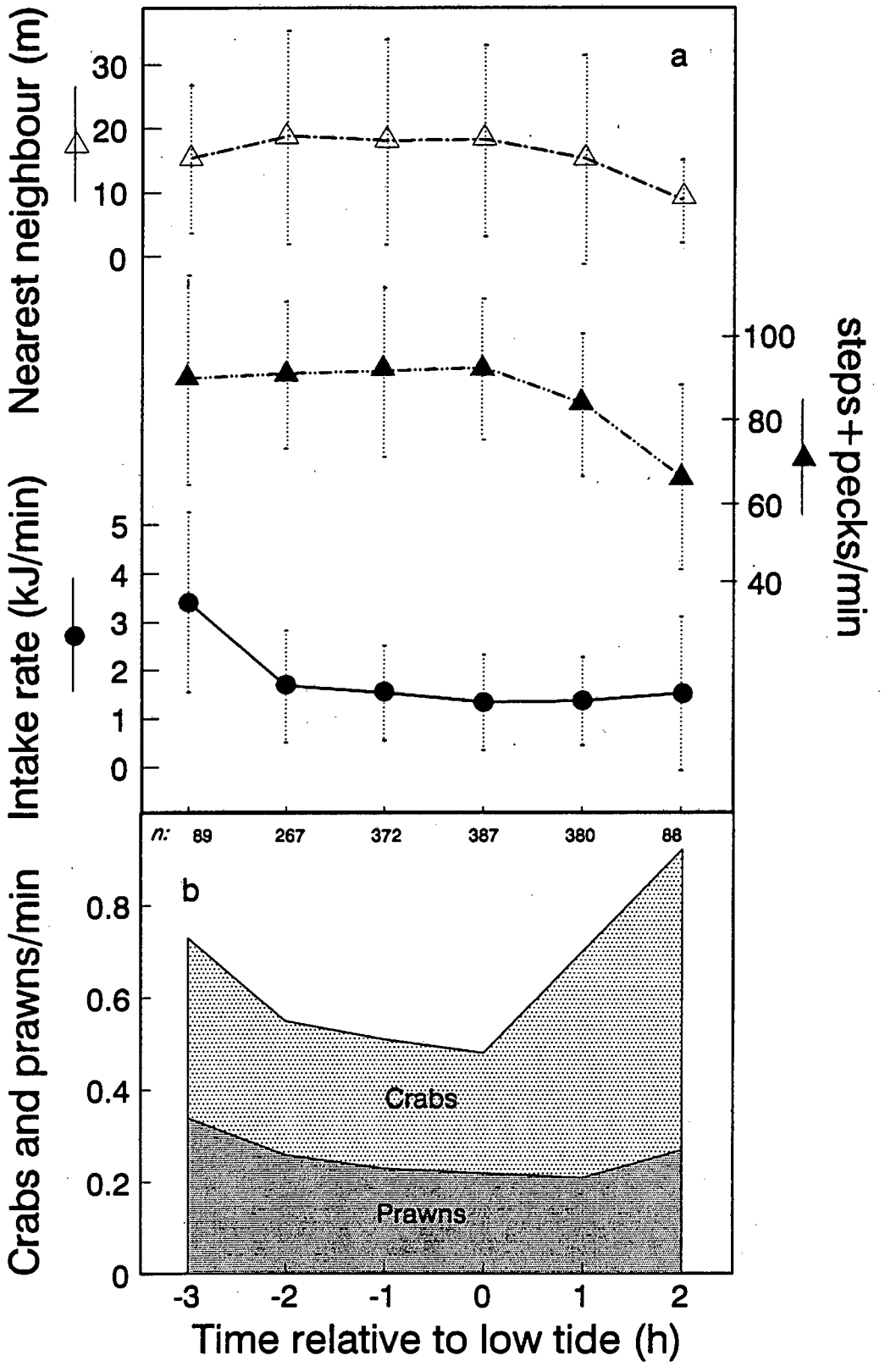


Figure 1.8. (a) Changes in mean (± S.D.) foraging speed (steps + pecks/min), nearest-neighbour distance (m) and net energy intake rates (kJ/min), and (b) changes in the numbers of crabs and prawns consumed per minute over the low tide exposure period, for spring and summer months combined.

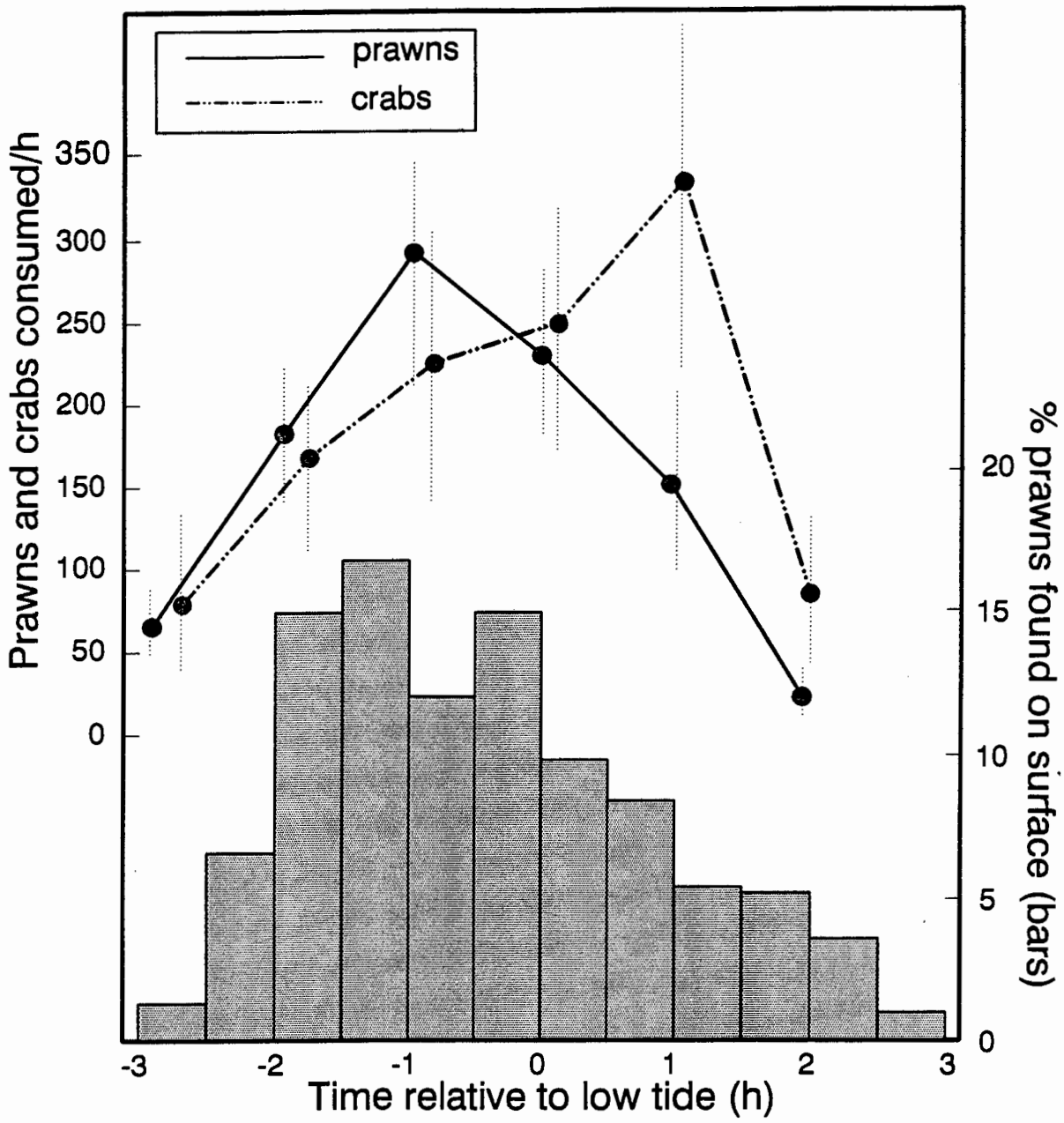


Figure 1.9. Changes in the numbers of prawns and crabs consumed per hour by Whimbrels over the low tide exposure period, and the percentage of total numbers of prawns emerging during the low tide period (after Martin 1991).

Seasonal patterns of prey availability, bird density and foraging success

The median number of surfacing prawns recorded per month by Martin (1991) showed a summer peak and winter trough, but there was a large amount of variability between sites as well as between months (Fig. 1.10a). However, there were no significant differences in prey availability between months (ANOVA, d.f. = 37, F-ratio = 1.55, $P = 0.18$). The difference between prawn numbers in the austral spring and summer (September to April) and the autumn and winter months (May to August) was not significant ($t = 1.96$, $P = 0.06$), but was possibly an artefact of small sample size. Martin (1991) found a significant correlation between numbers of prawns counted and air temperature ($r = 0.36$, $P < 0.02$), however the low coefficient of correlation suggests that the influence of temperature may be secondary to some seasonal pattern. The number of surfacing prawns was not related to their abundance in the sediment over the season, which peaked during winter (Martin 1991). During this study, the number of prawns found on the surface in $400m^2$ quadrats over one low tide period was significantly positively related to burrow density ($n = 15$, $r = 0.56$, $P < 0.05$; Fig. 1.11).

Because of the variation in prawn availability between microhabitats, the likelihood of day-to-day (possibly temperature-related) variability, and because many prawns only remain on the surface for a few minutes and the chances of missing them are high (Martin 1991), accurate quantification of prawn surfacing behaviour could only be achieved through a much more thorough study. Martin's (1991) median values of monthly prawn availability are presented, but should be interpreted with caution.

The mean densities of the crabs *C. edwardsii* (the main crab species eaten by Grey Plovers and Whimbrels on the study area) and *S. catenata* (eaten by Whimbrels in the saltmarshes) at the Zwartkops estuary peak in mid- to late summer (Els 1982; Fig. 1.10b).

Because Grey Plovers defended fixed territories on the study area during the austral summer, their densities were constant from day to day during this period. Densities on the study area closely followed seasonal changes in densities on the estuary (Fig. 1.12a). The average distance to the nearest conspecific neighbour was inversely related to bird density ($n = 7$, $r = -0.84$, $P < 0.05$; Fig. 1.12a).

Although there were similar numbers of Whimbrels on the estuary in 1990 and 1991 (Fig. 1.3), the densities on the study area were considerably higher in the summer of 1990 than 1991 (Fig. 1.12b) and, despite the steady increase in Whimbrel numbers on the estuary from September 1991, their density on the study area remained low until November. The mean monthly number of Whimbrels foraging on the study area (mean F_{max}) formed a variable proportion of the total number on the Main section. Mean F_{max} was 24% of the Main section population in February 1990 and 33% during

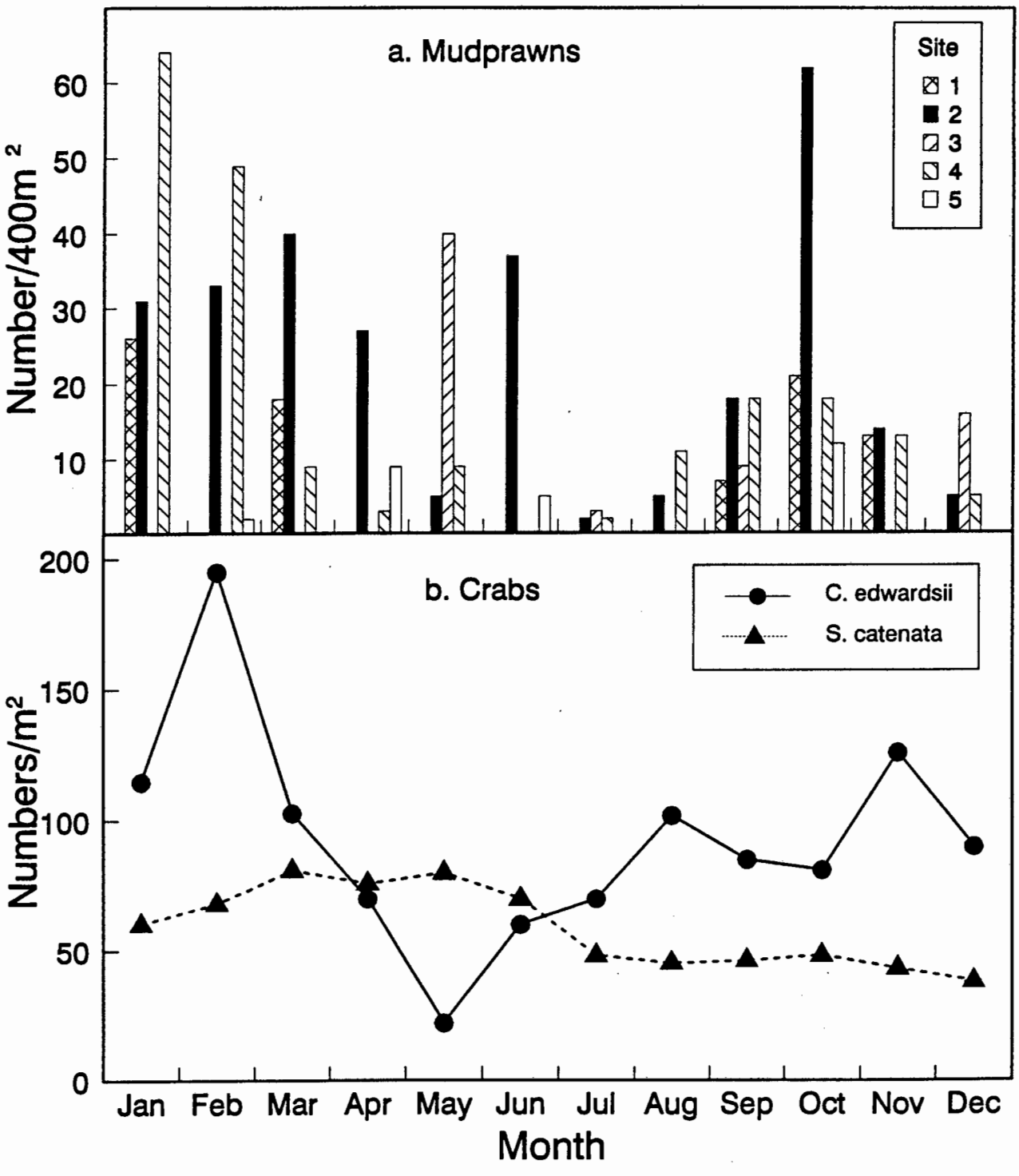


Figure 1.10. (a) Seasonal variation in the numbers of *Upogebia* prawns found on the surface per low tide period per 400m^2 plot at five sites along the Zwartkops estuary (A.P. Martin, unpublished data); and (b) seasonal variation in the mean density of two dominant crab species at the Zwartkops estuary, *Cleistostoma edwardsii* and *Sesarma catenata* (after Els 1982).

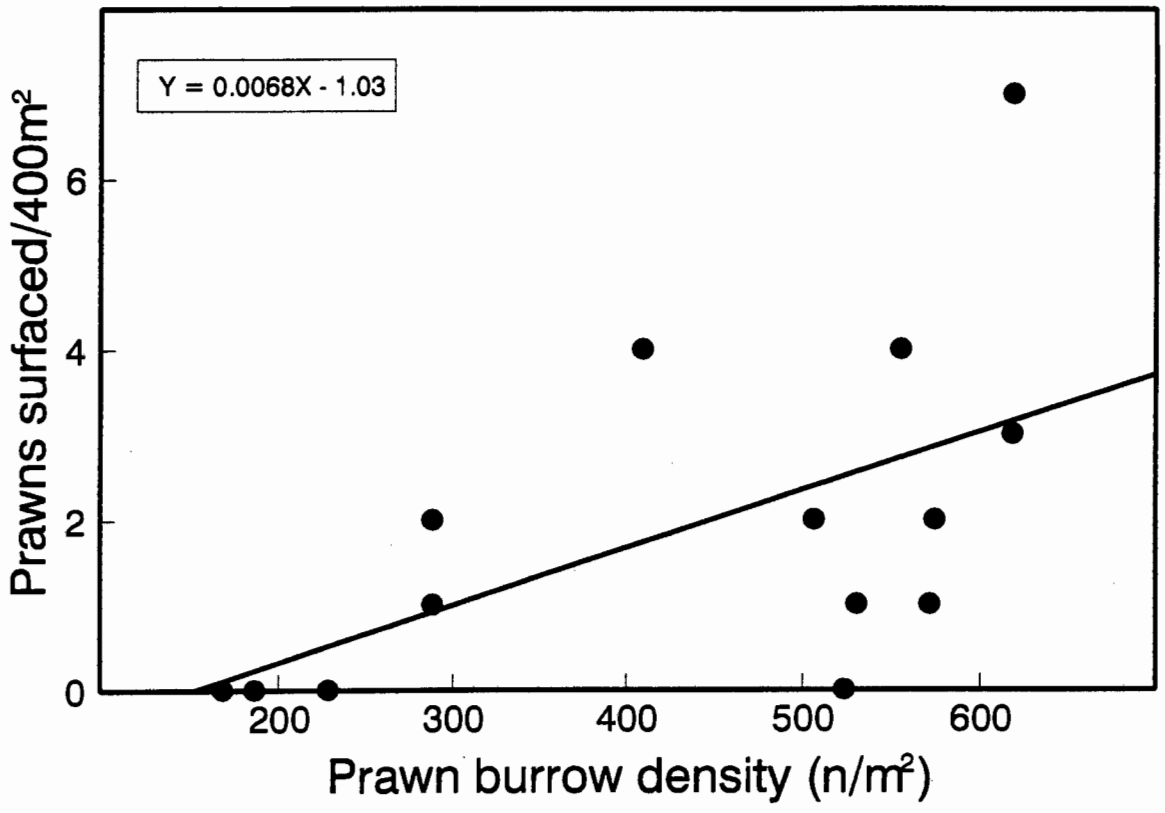


Figure 1.11. Relationship between the number of prawns found on the surface in $400m^2$ plots over the low tide period and the density of burrows in each plot.

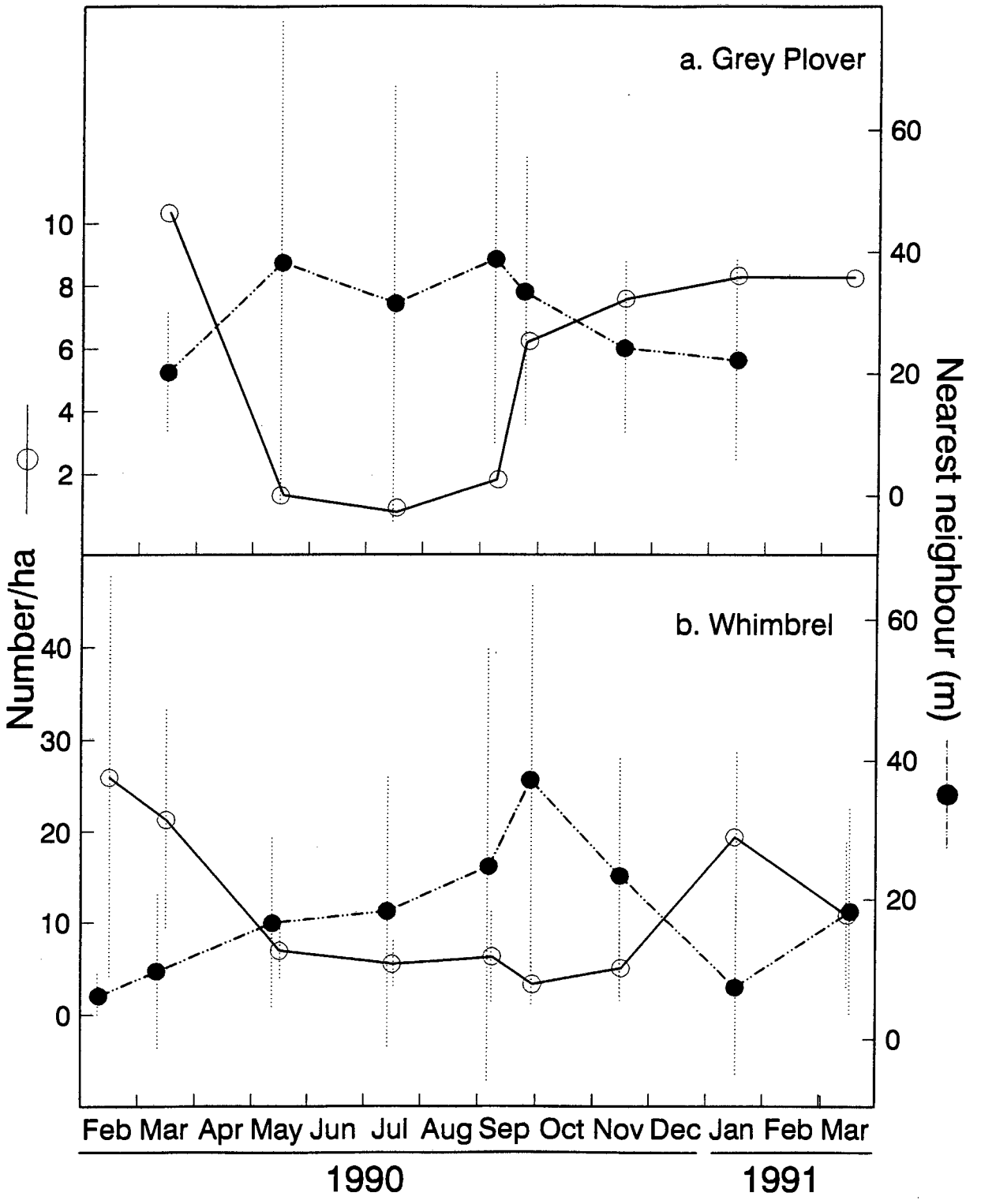


Figure 1.12. Seasonal changes in the mean (± S.D.) densities (n/ha) and nearest-neighbour distances of (a) Grey Plovers and (b) foraging Whimbrels on the study area.

winter. This decreased to 19% in early September, and 5% and 6% in late September and November respectively, before rising to 16% in January and 19% in March.

Mean nearest-neighbour distance for Whimbrels (Fig. 1.12b) was inversely and linearly related to the mean number of Whimbrels foraging on the study area ($n = 9$, $r = -0.88$, $P < 0.01$), as well as to the mean total number of Whimbrels (foraging and resting; $n = 9$, $r = -0.85$, $P < 0.01$), indicating an even rather than clumped distribution of individuals.

Energy intake rates of Grey Plovers and Whimbrels were low during the summer months (January to March; Fig. 1.13). Whimbrel intake rates were lowest in February 1990 (Fig. 1.13b), when the highest densities of birds were present on the study area (Fig. 1.12b). Grey Plover intake rates remained low during winter (May - July), but those of Whimbrels increased considerably from the end of summer. Intake rates of both species were highest during spring (September - November, Fig. 1.13).

The number of prawns consumed per hectare by Grey Plovers and Whimbrels over the low tide period was calculated from prawn intake rate, mean foraging time, and mean numbers of birds foraging over the low tide period. The seasonal patterns of numbers of prawns consumed was comparable with the seasonal pattern of surface prawn abundance found by Martin (1991; Fig. 1.14). The numbers of prawns consumed per hectare per low tide period by Whimbrels were significantly positively correlated with the median numbers counted on the surface ($r = 0.83$, $n = 8$, $P < 0.05$), which possibly verifies the seasonal pattern of availability. However, the combined consumption by Grey Plovers and Whimbrels exceeds Martin's (1991) estimates of availability, suggesting that the latter were underestimated.

The seasonal changes in energy intake rates of Grey Plovers and Whimbrels did not follow trends in prey availability, except that both increased during the spring arrival period. Low prey availability in winter was, however, reflected in low energy intake rates of Grey Plovers, and the relatively high proportion of prawns which Whimbrels obtained by tactile probing. In May and July, 15 and 14% of prawns were captured tactilely, compared with 2, 6, 8 and 5% in the following September, November, January and March.

The energy intake rates of Grey Plovers during the summer months were negatively correlated with the average number of birds on the study area ($n = 5$, $r = -0.93$, $P < 0.05$), and Whimbrel energy intake rates were strongly correlated with mean nearest-neighbour distance throughout the year ($n = 9$, $r = 0.80$, $P < 0.01$), intake rates being highest when the density of conspecifics was lowest.

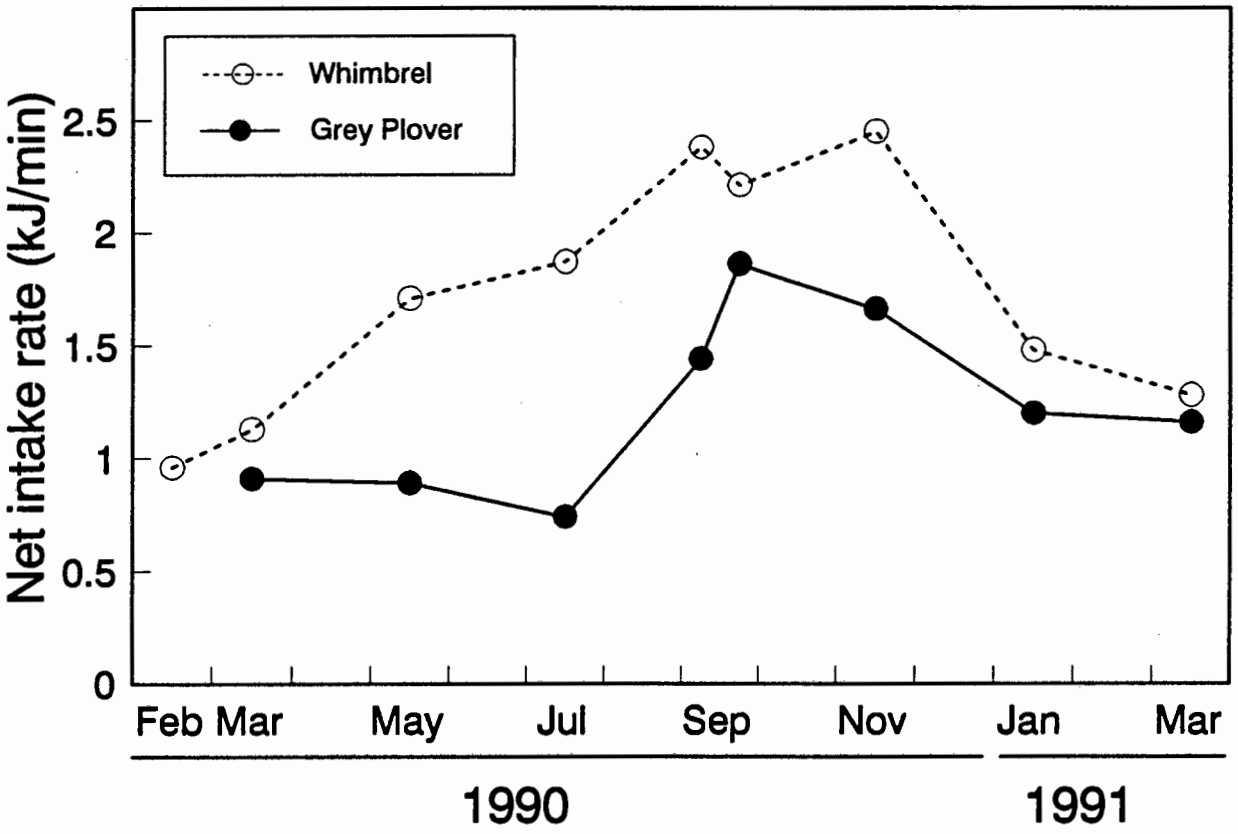


Figure 1.13. Seasonal variation in the net energy intake rates (kJ/min) of Whimbrels and territorial Grey Plovers at the Zwartkops estuary.

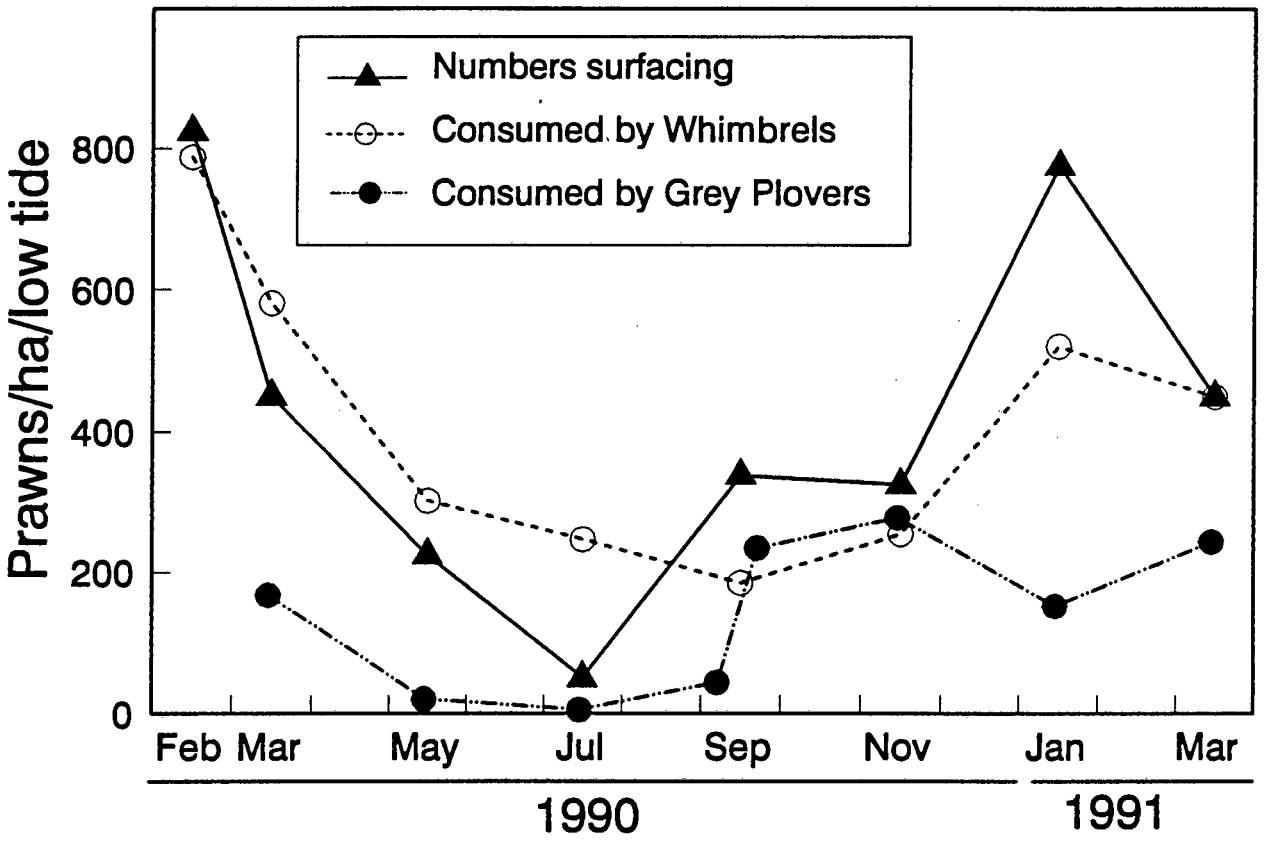


Figure 1.14. The median number of prawns found on the surface per ha per low tide period (after Martin 1991), and the mean numbers of prawns consumed per ha per low tide period by Grey Plovers and Whimbrels.

Foraging effort and daily energy intake

Foraging effort was measured as foraging speed (step and peck rates) and foraging time. Mean step rate varied very little from month to month for both species (Fig. 1.15). Grey Plover peck rates were significantly higher in winter and the first half of September than during the rest of the year (ANOVA $_{7,1456}$, Tukey test, $P < 0.001$). Whimbrel step rate was significantly lower during the second half of September than at other times, and significantly higher in January and March 1991 than during the previous spring (late September and November) and summer (February and March 1990; ANOVA $_{8,2148}$, Tukey test, $P < 0.001$). Whimbrel peck rates were significantly higher during winter (May and July) than in other months (ANOVA $_{8,2148}$, Tukey test, $P < 0.001$). High peck rates of Grey Plovers and high step and peck rates of Whimbrels occurred in months when the proportion of immature birds in the population was high (May to early September).

Grey Plovers were almost always present on their territories from the time they became exposed, or just shallow enough to stand in, until the incoming tide forced them to depart. The average amount of time spent foraging during the daytime low-tide period by Grey Plovers was fairly constant throughout the season (Fig. 1.16) and was unrelated to the duration of tidal exposure. However, unusually short exposure periods reduced their foraging time in July and January (Fig. 1.16).

The average amount of time that Whimbrels spent on the study area per day was related to the duration of the exposure period (Fig. 1.16, $n = 8$, $r = 0.80$, $P < 0.05$). The average time spent foraging by Whimbrels per low tide period ranged from 135 to 181 minutes, and was also related to the duration of exposure ($n = 8$, $r = 0.72$, $P < 0.05$). Resting time (roosting, standing and preening between foraging bouts) accounted for 5 - 28% of the time the birds were present on the study area, and was highest in spring and in February 1990. Apart from the spring months (September - November), the percentage of time spent resting increased as the number of Whimbrels present on the study area increased ($n = 6$, $r = 0.83$, $P < 0.05$).

At night, Grey Plovers foraged for 82 - 87% of the time spent foraging during the daytime low tide period (Table 1.4). During July, numbers foraging at night were significantly lower than during the day (Wilcoxin test for matched pairs, $n = 14$, $T = 2$, $P < 0.05$). The effective average foraging time per individual at night in July was thus calculated as the ratio of the nocturnal to diurnal foraging population (5/7.5, Table 1.4) multiplied by the calculated nocturnal foraging time, and was 57% of daytime foraging time. In the other months, all Grey Plovers on the study area defended fixed territories, and were present by day and night.

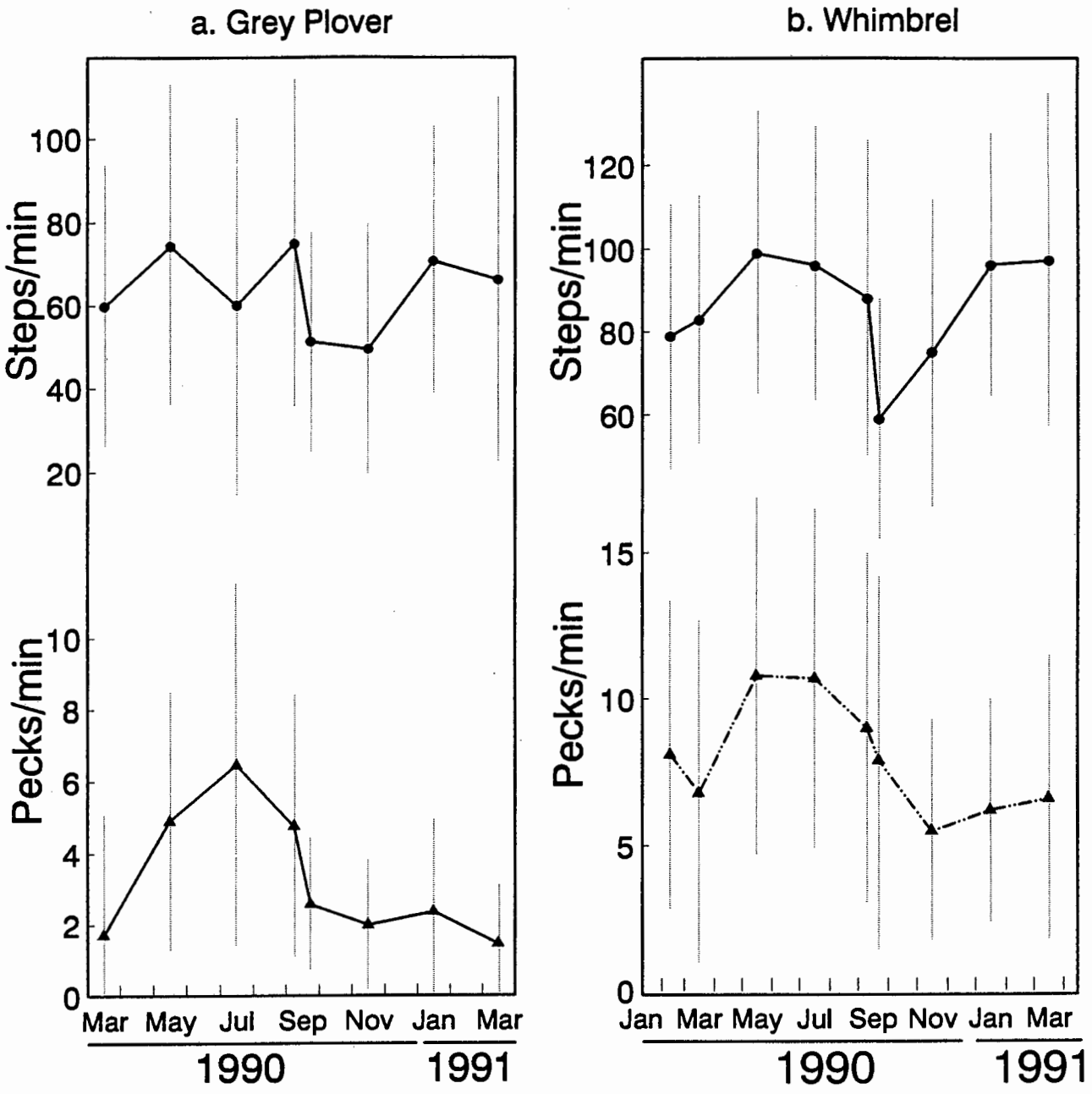


Figure 1.15. Seasonal changes in the mean (± S.D.) numbers of steps and pecks taken per minute by (a) Grey Plovers and (b) Whimbrels.

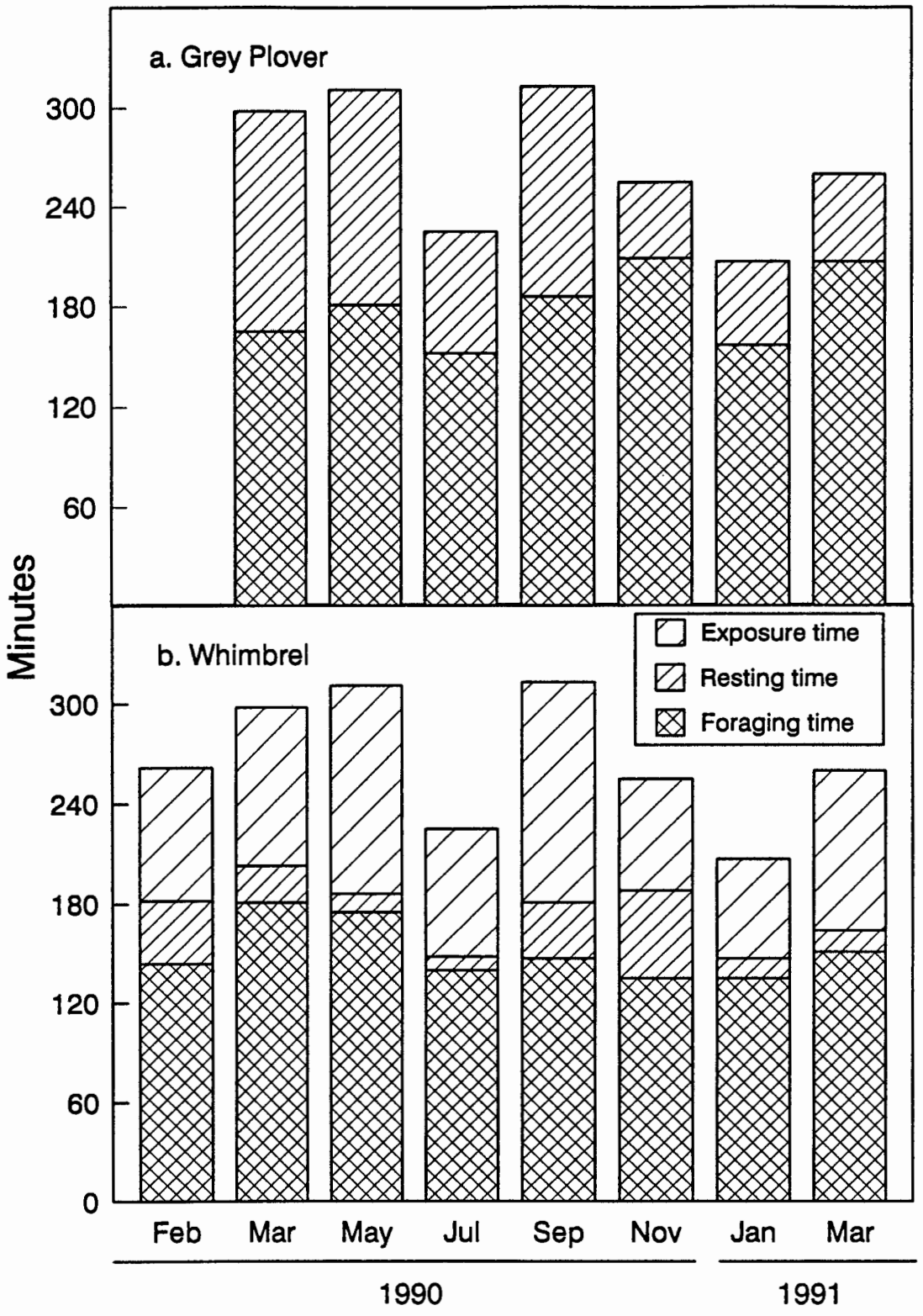


Figure 1.16. The mean duration (minutes) of tidal exposure recorded during the study in different months, and superimposed, the mean foraging and resting time of (a) Grey Plovers and (b) Whimbrels over the low tide period.

Table 1.4. Mean low tide foraging population (F_{max}) and individual foraging time (minutes) by day and night, and the daily total time spent foraging (minutes) during four months in 1991.

Month	DAY Mean F_{max}	Foraging time	NIGHT Mean F_{max}	Foraging time	Total low tide foraging time
GREY PLOVER					
July	7.5	149	5.0	128	234*
October	8	153	8	133	286
December	9	190	9	159	349
March	12	195	12	160	355
WHIMBREL					
July	9.5	100	3.5	43	116*
October	4.3	133	7.0	129	211*
December	13.0	158	12.5	106	264
March	18.7	181	23.0	165	346

* Denotes cases when the numbers of birds foraging by day and night were significantly different, thus assuming the larger F_{max} to represent the foraging population, foraging time for the period (day or night) in which F_{max} was lower was reduced proportionally.

The numbers of Whimbrels foraging by day and night were not significantly different during the summer months of December 1991 and March 1991 (Table 1.4; Chapter 3), and nocturnal foraging accounted for 40% and 48% of total low tide foraging time respectively. In July the number of birds foraging at night was significantly lower than by day (Wilcoxon's Test for matched pairs, $n = 14$, $T = 0$, $P < 0.01$). The overall nocturnal contribution to daily average foraging time was thus 14% in July. In October, significantly more Whimbrels foraged by night than by day ($n = 14$, $T = 15$, $P < 0.05$). These additional birds may have foraged elsewhere by day, but if it is assumed that they did not, then nocturnal foraging time accounted for 61% of the daily total.

Daytime Whimbrel foraging numbers were higher in July 1990 than July 1991 (mean 7.9 vs 3.3) and were higher in September and November 1990 than October 1991, (mean 7.0 and 7.0 *vs* 4.0). Because higher densities may have resulted in lower foraging success, nocturnal foraging in winter and spring may have been more important in 1990 than in 1991, but no quantitative nocturnal observations were made in 1990.

Table 1.5. Seasonal changes in the percentage of immature birds (imm) in the population, the expected average daily net energy requirements (DER) per individual (all age classes combined), and the percentage of these requirements gained during the daytime low tide period by Grey Plovers and Whimbrels. In calculating average energy requirements of the population, the assumption was made that the energy requirements of immature birds (probably comprising 2nd year as well as juvenile birds) was the same as calculated for juveniles.

Month	Grey Plover			Whimbrel		
	% imm	DER	% gained by day	% imm	DER	% gained by day
Feb 1990		no data		28	598	24
Mar	3	399	38	28	598	34
May	100	324	50	100	473	63
Jul	100	324	35	100	473	55
Sep1	23	332	79	60	490	69
Sep2	7	333	106	43	498	66
Nov	5	334	104	36	500	66
Jan 1991	4	367	51	26	553	36
Mar	4	398	62	39	578	34

The percentage of estimated daily energy requirements gained during the daytime low tide period varied substantially through the year for both Grey Plovers and Whimbrels (Table 1.5). During spring (September to November 1990), when energy intake rates were highest, both Grey Plovers and Whimbrels gained a high proportion of their requirements during the daytime. The relatively low daytime intakes recorded in July and January for both Grey Plovers and Whimbrels were due partly to the shorter tidal duration and foraging times (Fig. 1.16). Daytime intake was generally lowest during the premigratory period (Fig. 1.13). However, adult Whimbrels obtained 46% of their estimated daily requirements during the day in March 1991, indicating that the deficit for adults was less than for immature birds. Grey Plovers achieved a greater proportion of their energy requirements during the daytime low-tide period than Whimbrels, but Whimbrels gained part of their daily energy intake by foraging in the saltmarshes during high tide. The actual contribution of high-tide foraging to energy intake could not be quantified.

Aggressive behaviour

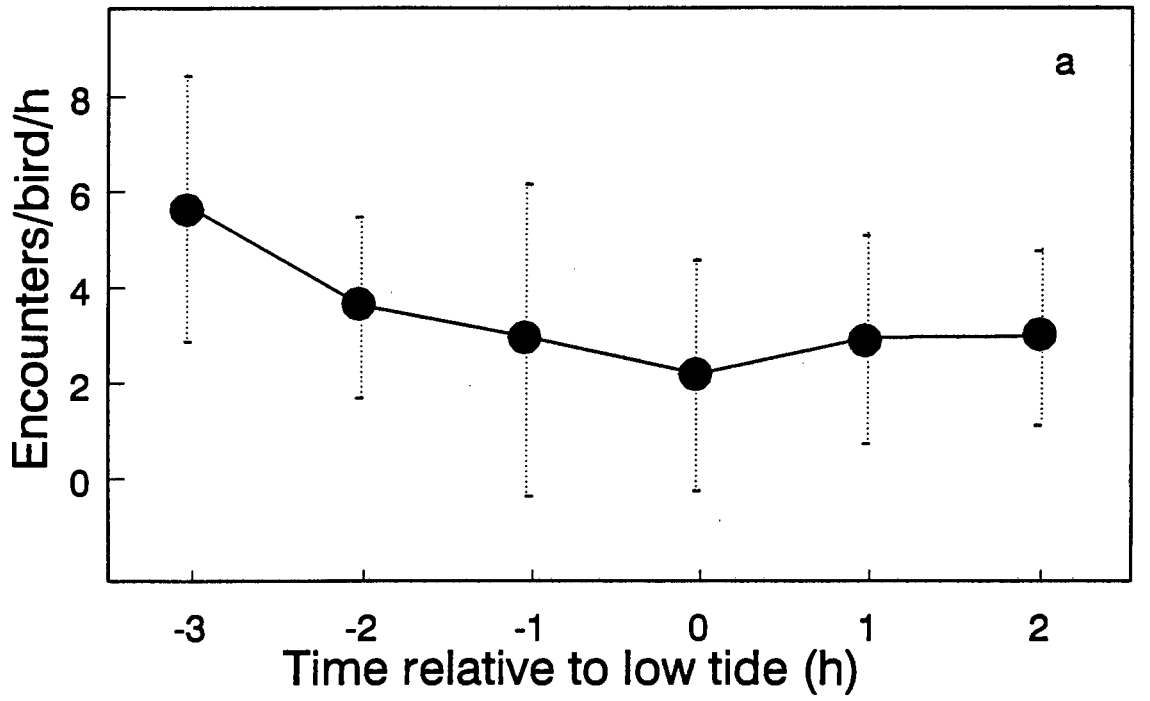
Grey Plovers defended territories throughout the austral summer, and their aggressive behaviour is examined separately in Chapter 3.

Most Whimbrel aggression was nonterritorial, and encounters were of short duration. The four different types of nonterritorial encounters lasted on average 1.6 ± 0.7s (type 1, n = 18), 3.3 ± 2.5s (type 2, n = 164), 3.8 ± 3.0s (type 3, n = 114) and 3.0 ± 1.5s (type 4, n = 6).

Whimbrels were usually most aggressive shortly after their arrival on the study area as the tide was receding (Fig. 1.17a), when nearest neighbour distances were smallest, and energy intake rates highest (Fig. 1.8a).

Seasonal changes in Whimbrel aggression rates (Fig. 1.17b) did not follow patterns of either nearest-neighbour distance, density of Whimbrels on either the estuary or the study area, or energy intake rates (Figs. 1.3, 1.10 and 1.12). Encounters were rare amongst the immature birds during winter, when overall densities were low and the birds foraged in loose aggregations. Aggression rates were fairly constant during the summer months, except for a peak in February 1990, when the number of birds on the study area was maximal, and another peak during the second half of September, when nearest neighbour distances were greatest. The high rate of aggression during late September coincided with a change in behaviour. The majority of Whimbrels foraged nonterritorially throughout most of the year at the Zwartkops estuary. However, during the arrival period, territorial behaviour was commonly observed on the estuary. Territorial behaviour on the study area was usually limited to one colour-ringed individual which persisted in this behaviour from September to November, and for a short period, a second individual during September. This behaviour was more prevalent on the larger expanses of mud in neighbouring areas. Many Whimbrels commenced defence of large territories of *ca.* 0.5 - 0.75 ha, and neighbouring birds engaged in lengthy parallel runs along their boundaries. Most of these territories had dissolved by November.

Seasonal changes in the mean intensity of aggressive encounters were closely linked to the encounter rate (n = 9, r = 0.96, $P < 0.001$, Fig. 1.17b).



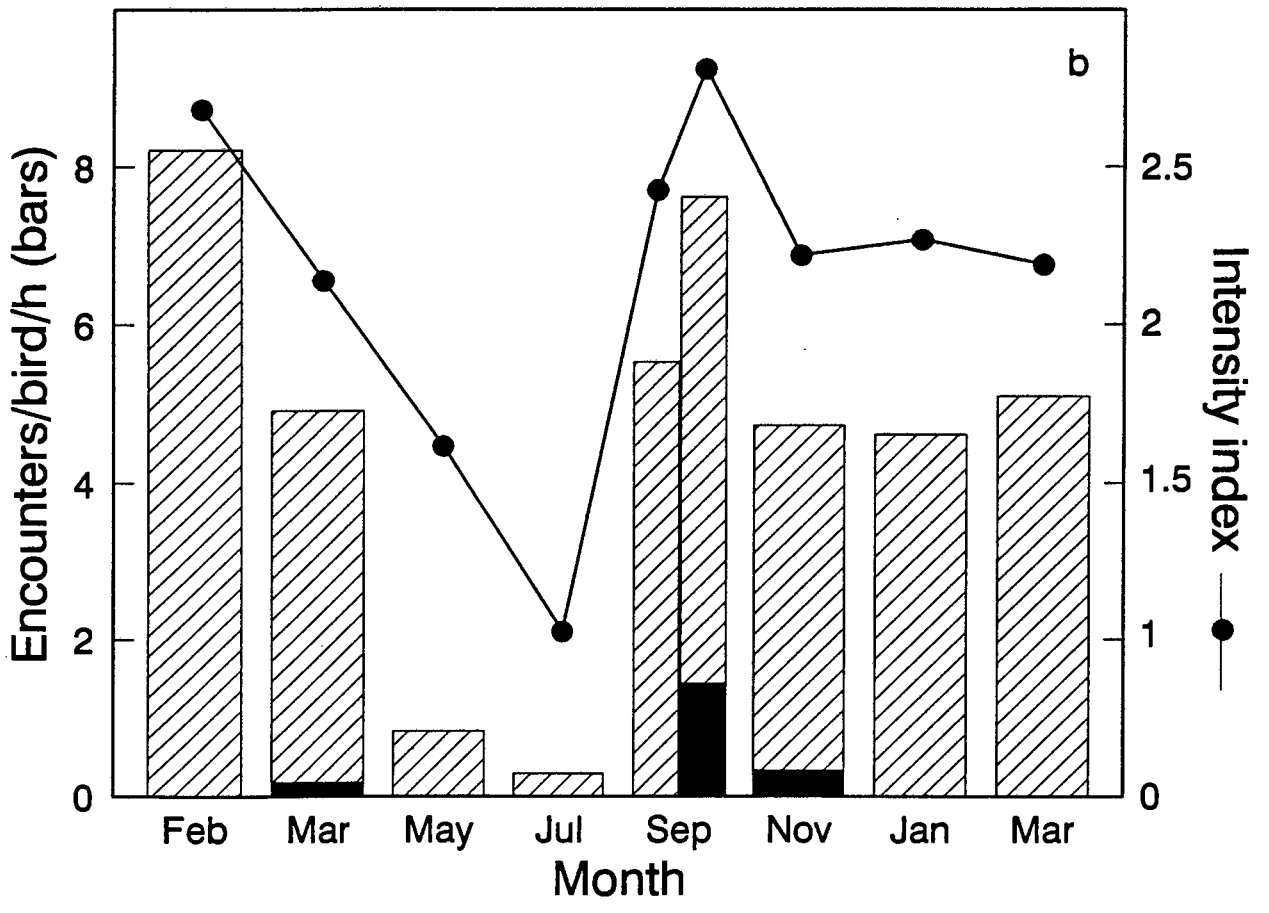


Figure 1.17. (a) Variation in mean aggressive encounter rate (spring and summer months combined) over the low tide exposure period, and (b) seasonal changes in the mean number of aggressive encounters per bird per hour, with territorial encounters shaded black, and the mean intensity of encounters.

DISCUSSION

Distributional evidence for competition

Grey Plover and Whimbrel densities ranged from low in winter to high during the premigratory period. Their relative abundance in different sections of the estuary reflected the distribution of prawn biomass (Fig. 1.4). The density of waders has frequently been found to be correlated with prey supplies (e.g. Hulscher 1976, Goss-Custard, Kay & Blindell 1977b, Bryant 1979, Martin 1991), but the tendency to concentrate disproportionately in richer foraging areas is expected to decrease as bird densities and competition increase (Goss-Custard 1977b, Zwarts 1981). Grey Plover numbers during winter were only 3% of the summer population, and these birds congregated in the richest section of the estuary. Arriving Grey Plovers concentrated in this area, which filled up at a faster rate than the other sections of the estuary (Table 1.1, Fig. 1.5). The overwintering population of Whimbrels was proportionally much larger than that of Grey Plovers, and these birds occupied all sections of the estuary, concentrating mostly in the two richest sections. Considering the low availability of prawns during winter, Whimbrel numbers may have been sufficiently high that competition would be increased by further aggregation in the preferred areas. By late September, Whimbrels concentrated in the Main section, and the proportion of the population in this area decreased as the population increased further. In addition, there was greater variance in bird numbers on the poorer than the richer sections of the estuary. During the summer, Whimbrels, which were predominantly nonterritorial, appeared to respond to local changes in prey availability, in that the proportion of the Main section population that foraged on the study area was fairly variable. These patterns demonstrate a sequential filling of habitats at the Zwartkops estuary in relation to prey supplies. This suggests that Grey Plovers and Whimbrels were minimising intraspecific competition for resources, which, conversely, implies that competition exists among both Grey Plovers and Whimbrels on the estuary.

Do Grey Plovers compete with Whimbrels for food?

There was no evidence of any spatial separation of Grey Plovers and Whimbrels on the estuary, and Whimbrels foraged within the territories of Grey Plovers. This, and the fact that the birds consume the same species and size classes of prey, suggests that interspecific competition for resources may not be strong. Nevertheless, the fact that the same size classes of prawns are consumed by both species can be at least partly explained by the fact that prawns are taken as they are encountered on the surface, and there is thus no prior criterion for selecting size classes, such as, for example, burrow size.

The seasonal trends in the numbers of prawns consumed relative to their patterns of availability (Fig. 1.14) suggest that Grey Plovers and Whimbrels were taking most available prawns on the surface (other than those taken to a much lesser extent by Kelp Gulls *Larus dominicanus*, Common Terns *Sterna hirundo*, Turnstones *Arenaria interpres*, Greater Sandplovers *Charadrius leschenaultii*, Curlews *Numenius arquata* and Terek Sandpipers *Xenus cinereus*).

The average net energy yield from prawns taken by Whimbrels (6.0 $\pm$ 4.5 kJ, n = 530) was more than ten times greater than from crabs, but because mean handling time was long (8.1 $\pm$ 9.3 s, n = 380), they were only about 44% more profitable than crabs in terms of the net energy gain per unit handling time (0.75 vs 0.52 $kJ.s^{-1}$). Grey Plovers took longer to handle prawns than Whimbrels (19.3 $\pm$ 20.7 s, n = 184; Fig. 1.6), and frequently broke the larger prawns into pieces before swallowing them. Prawns were thus less profitable per unit handling time than crabs for Grey Plovers. The fact that both Grey Plovers and Whimbrels eat both prawns and crabs therefore suggests that the rate at which they encountered their respectively more profitable prey species was insufficient to allow for prey specialisation; with the above profitability values, an (impossible) encounter rate with prawns of at least $9.min^{-1}$ is required to allow Whimbrels to specialise on them (Pulliam 1974, Krebs & Davies 1981). Although the small crabs are highly abundant (Fig. 1.10b), they are difficult to see (at least to the human observer), and usually were taken most frequently on the incoming tide (Figs. 1.8 and 1.9), when their active foraging would have made them easier to detect. Thus potential for specialisation on crabs by Grey Plovers may have been hindered by their comparative crypticity relative to prawns - see Krebs (1980). Similarly, the increase in tactile foraging by Whimbrels during winter suggests that the combined encounter rate of surface prawns and crabs was too low to sustain specialisation on surface-active prey.

The overlap in prey taken by Grey Plovers and Whimbrels may thus be due largely to low encounter rates with their preferred prey, rather than due to a superabundance of prey, in which case the two species probably directly affect the foraging success of one another. Bell & Ford (1990) found that foraging niche overlaps between three Australian warblers (*Acanthiza* spp.) initially declined as food became scarce, then rose again when food supplies declined further, and suggested that they responded to persistent food shortage by expanding their foraging niche and risking greater interspecific competition. Grey Plovers were evenly spread throughout most of the mudflats due to their territorial behaviour, and may not have been able to exclude the larger Whimbrels from their foraging areas, and conversely, it may not have been worthwhile for Whimbrels to attempt to displace Grey Plovers.

Energetic evidence for competition

Evidence suggested that juvenile birds were less efficient foragers than adults, and although sample sizes were too small to show a significant difference in intake rates, their foraging effort was significantly greater. A lower foraging efficiency for juveniles may be the consequence of their inexperience, or due to competition from adults, which have higher energy requirements due to their larger body size and extra energy requirements for premigratory reserve deposition.

Although seasonal patterns of prey availability are almost certainly an important influence on intake rates, there was no direct relationship between the two, except during winter, when Grey Plover intake rates were low, and Whimbrels resorted to more tactile foraging (Fig. 1.12b). However, the importance of prey availability becomes apparent when the number of conspecifics sharing the same resource is taken into account (Figs. 1.9, 1.14).

The seasonal pattern of energy intake rate for both species was best explained by bird density, and a proximate measure of bird density, namely mean nearest-neighbour distance: this strongly suggests that birds were negatively affected by competition for resources. Intake rates of Grey Plovers and Whimbrels were probably also negatively influenced by the densities of one another, but as their densities followed similar seasonal patterns, the relative influence of intra- and interspecific competition could not be separated.

The depression of intake rates by the proximity of neighbours has been attributed to a negative influence of birds on the behaviour of prey (Goss-Custard 1970, Zwarts 1981, Selman & Goss-Custard 1988), as well as to increased interference between birds (Goss-Custard 1976, Zwarts 1978, Zwarts & Drent 1981). The influence of bird density on prey behaviour has not been investigated at the Zwartkops estuary, but it is likely that crabs respond to the presence of birds (e.g. by freezing or retreating into a burrow) as has been found elsewhere (e.g. Zwarts 1981, 1985). Bird density may not affect the surfacing behaviour of prawns since this is thought to be parasite-induced, but the birds' presence may cause prawns to re-enter burrows more rapidly. Grey Plovers are obligate visual foragers, and Whimbrels at the Zwartkops estuary forage predominantly visually. Their search area was fairly large, as evidenced by their frequently running up to five metres or more to capture a prawn. Visually foraging birds are likely to be prone to interference by increased neighbour encroachment into their search area at higher densities, and intake rates will be further depressed by the increased chance of neighbours 'spotting' the same prey.

Foraging speed did not vary greatly in relation to energy intake rates and requirements, and much of the seasonal variation in foraging effort could be explained by the proportion of immature birds in the population. The slight increase in foraging

speed over the summer months may have been a consequence of increasing difficulty in finding prey, but the extent to which this increase in effort may have increased intake rates is impossible to determine. Whimbrel step rates were higher in the summer of 1991 than 1990, perhaps because of the greater distance between neighbours, but their peck rates were higher during 1990, possibly due to increased tactile foraging at high conspecific densities.

The daily energy requirements of birds vary with age and season, but their total daily intake is limited by a combination of their intake rate and the available foraging time. Turnstones in Scotland (Metcalfe & Furness 1984) and Whimbrels in Mauritania (Zwarts 1990) increase their intake rate in response to increased energy requirements prior to migration. In the latter case this was shown to be possible because of increased prey availability. Waders are likely to maximise intake rates at all times (Goss-Custard 1985), and daily intake can only be increased to meet the increased premigratory energy demands by foraging for longer (e.g. Puttick 1980, Zwarts, Blomert & Hupkes 1990b), sometimes at the cost of reduced vigilance (Metcalfe & Furness 1984).

There was no time of year at which Grey Plovers or Whimbrels at the Zwartkops estuary foraged for close to 100% of the available daytime low tide period. Whimbrels that left the study area before the end of the exposure period usually joined roosting flocks in a nearby creek, and, although observed occasionally, it is unlikely that many birds left the study area in order to forage elsewhere. Moreover, Whimbrel numbers on the study area followed the temporal variation in prey availabilty as well as the change in exposed mudflat area, resulting in little variation in nearest-neighbour distances. This suggests that individual Whimbrels spent as long as possible on the intertidal foraging areas. Grey Plovers spent all the time possible on their territories, but this may also be explained as being necessary for territory defence *per se*. Large wader species tend to forage for a lower proportion (60 - 85%) of the exposure time than small waders, which usually forage for more than 90% of tidal exposure time (e.g. Engelmoer *et al.* 1984), probably due to the relative scaling of bird and prey size (Goss-Custard, Jones & Newbery 1977a, Lifjeld 1984), and an increased proportion of time needed for digestive pauses when consuming larger prey (Zwarts *et al.* 1990b). The maximum proportion of daytime exposure time used for foraging by Whimbrels at the Zwartkops was 64%, compared with 80 - 85% for Whimbrels in Mauritania (Zwarts *et al.* 1990b). Whimbrels consumed comparatively large prey at the Zwartkops, and foraged at higher densities than in Mauritania (Zwarts *et al.* 1990a).

During July and January, exposure periods were reduced by low pressure weather systems. On some days (all but one in January), the mudbank did not expose to its full area, and the majority of birds foraged in shallow water. Thus Grey Plover and Whimbrel foraging time was shorter than expected in both July and January. The

reduced foraging time in summer 1990, when Grey Plover and Whimbrel densities were highest, and the relationship between Whimbrel resting time and bird density, is consistent with the findings of Zwarts & Drent (1981) that the proportion of Eurasian Oystercatchers *Haematopus ostralegus* foraging was reduced at high densities. Thus, there was no evidence that Grey Plover or Whimbrel foraging time was adjusted in relation to seasonal changes in energy intake rates or energy demands.

Although daytime low tide energy gain by Grey Plovers and Whimbrels at the Zwartkops estuary was high during parts of the year, there were periods, particularly before northward migration, and especially for Whimbrels, when the energy obtained was much less than their predicted daily requirements. The larger deficits for Whimbrels may be explained by the fact that they supplemented their low tide intake throughout the year both by foraging for part of the high tide period in the adjacent saltmarshes. Foraging in the saltmarshes, where there is a high biomass of the relatively large crab *S. catenata* (Baird & Winter 1979, Els 1982), probably provides a significant proportion of Whimbrels' daily energy intake at the Zwartkops. However, this activity appeared to be limited largely to the period from when the saltmarshes are wet enough to bring the crabs to the surface, to when they are flooded. Energy intake from the saltmarshes is likely to be most important during neap tide periods, when the extent and duration of mudflat exposure is reduced.

Nocturnal foraging was important in satisfying the daily energy requirements for both Grey Plovers and Whimbrels; both species foraged at night throughout the year. Diurnal and nocturnal intake rates were not significantly different (Chapter 3). During summer, when intake rates were low and premigratory energy demands high, both species foraged as much by night as by day. Considering the high energy intake rates observed in spring 1990, it was surprising that birds spent at least as much time foraging at night as during the day in October 1991. Shorebirds in southern Africa do not build up fat reserves for the nonbreeding season as they do in cold north temperate regions (Summers & Waltner 1979; Table 1.2). However, their immediate post-migration energy requirements may be higher than was calculated, to make up for weight loss *en route*. This is supported by the increased amount of nocturnal foraging by shorebirds at the Berg River estuary, South Africa, in spring as well as autumn, compared to midsummer (Kalejta 1991). Furthermore, the low weights of Whimbrels in mid-primary moult in December suggests that energy requirements may be higher during moult; these birds could have suffered a small energy deficit at this time as a result. Juveniles are often more susceptible than adults to increased interference at higher densities (Goss-Custard & dit Durrell 1988), and are likely to have suffered greater energy deficits than adults during the premigratory period, when the density of birds and adult energy requirements were high.

Although the negative influence of bird densities on energy intake rates of Grey Plovers and Whimbrels suggest that competition is pronounced at the Zwartkops estuary, particularly when bird numbers are high towards the end of summer, the amount of energy gained during the daytime, the supplementary intake by Whimbrels during high tide and the fact that birds forage at night throughout the year, suggest that the birds did not suffer severe energy deficits at any time of the year. However, energy requirements may have been higher during the post-migratory period than calculated. Birds occupied the mudflats maximally during the low tide period, and foraging effort did not change appreciably through the year. This, coupled to the extent to which birds foraged at night, suggests that they may have been foraging maximally for most of the residence period, and that daily energy requirements were not met with ease.

Behavioural evidence for competition

Aggression rates frequently are a function of bird density (Hamilton 1959, Recher & Recher 1969, Goss-Custard 1977, Burger, Hahn & Chase 1979), although suppression of aggression at very high densities has been found in some tactile-foraging, flocking species (Harrington & Groves 1977, Burger *et al.* 1979, Puttick 1979, Kalejta 1991). Aggression rates amongst Whimbrels at the Zwartkops estuary were lowest in winter when the population was smallest, and peaked in February 1990, when densities were higher than in summer of the following year. High aggression rates may have a significant negative influence on energy intake rates, not because of loss of foraging time (most encounters were very short), but due to disturbance and eviction from the better foraging areas (encounters resulted in the victim's moving 0.5 to 60 m [mean = 14.8 $\pm$ 22.5m, n = 45]).

Aggression among Whimbrels did not increase with bird density through the season. High rates of aggression occurred in September, when nearest neighbour distances were greatest. This was in part a consequence of the Whimbrels' increased tendency for territorial behaviour in spring. Territorial behaviour may have been inhibited later in the season by the high densities of conspecifics on the estuary. The high rate of aggression in September (Fig. 1.15) may also reflect the establishment of a dominance hierarchy amongst newly-arrived individuals. Increasing familiarity resulting in decreasing aggression rates between territorial Grey Plovers was clearly evident over the season (Chapter 2). Although mostly nonterritorial, colour-ringed and other recognisable Whimbrels at the Zwartkops tended to be site faithful in their foraging (within and between years). Thus the fairly constant, rather than increasing, rate of aggression through the summer may have been the result of a similar process of neighbour familiarization, and indicates some degree of suppression of aggressive

behaviour. The higher frequency of aggression at the beginning of the exposure period may have been partly due to a daily re-establishment of dominance hierarchies, as well as the smaller nearest-neighbour distances at this time. Although aggression rates were partly related to Whimbrel densities between seasons, much of the variation in this behaviour was due to social factors and the length of time that individuals had foraged in proximity. Instantaneous measures of aggression rates are therefore not always a reliable indicator of the level of competition.

Why are Whimbrel densities so high at the Zwartkops estuary?

The overall density of Whimbrels across the Zwartkops estuary reached a peak of 4.5 birds.ha^{-1} during this study, and densities of up to 7.7 birds.ha^{-1} have been recorded in the past. The Main section supported densities of up to 8.6 birds.ha^{-1} during 1990-91, and foraging densities on the study area frequently exceeded 30 birds.ha^{-1} during summer. These densities are exceptionally high for Whimbrels. Territorial Whimbrels had a mean foraging density of 0.5 birds.ha^{-1} in their most favoured habitat on the Banc d'Arguin, Mauritania (Zwarts *et al.* 1990a), and of 1 bird.ha^{-1} in their preferred habitat in Guinea-Bissau (Zwarts 1985). In Panama, territorial Whimbrels foraged at a density of 1.1 birds.ha^{-1} (Mallory 1982). Foraging densities of Whimbrels on Mafia Island, Tanzania, however, reached 169 birds per kilometre of coastline (Bregnballe *et al.* 1990), representing densities which may have exceeded 3 birds.ha^{-1}. The maximum overall density of Whimbrels at the Zwartkops estuary exceeds the maximum overall density recorded at any other wetland in Africa by at least an order of magnitude (e.g. 0.44 birds.ha^{-1} in Guinea-Bissau, Smit & Piersma 1989; 0.42 birds.ha^{-1} at the Berg River estuary, Velásquez, Kalejta & Hockey 1991; 0.46 birds.ha^{-1} at Langebaan Lagoon, South Africa, Underhill 1987; and 0.43 birds.ha^{-1} at Mida Creek, Kenya, Bryant 1980).

Whimbrels are largely confined to the tropics during the nonbreeding season (Hayman, Marchant & Prater 1986), where they forage predominantly on crabs (Spain - Gunther 1963, Panama - Mallory 1981, India - Ali & Ripley 1969, South Korea - Piersma 1985, Mauritania - Zwarts & Dirksen 1990, Guinea-Bissau - Zwarts 1985, Seychelles - Summers 1980, Kenya, Madagascar and Mauritius - pers. obs.), and can be considered as 'plastic specialists' (*sensu* Morse 1980, Mallory 1981). Their numbers in southwestern Europe and in South Africa are very low by comparison with the tropics (e.g. Smit & Piersma 1989, Ryan *et al.* 1988). In South America, Whimbrels are also distributed largely within the tropics, except for a concentration in the Chiloe area of Chile (Morrison & Ross 1989). Whimbrels in central Chile are reported to eat mainly large polychaetes (Velásquez & Navarro 1993). In South Africa, both the Zwartkops estuary and Langebaan Lagoon (Christie & Moldan 1977)

support a high biomass of prawns. These are the only two South African coastal wetlands that also support large numbers of Whimbrels (up to 770 at Langebaan (1 700 ha), Underhill 1987). Thus the numerical distribution of Whimbrels is probably linked to the abundance of large, preferably surface-active, prey animals.

The unusually high density of Whimbrels at the Zwartkops estuary is probably a result of both the abundance of *Upogebia* and the large area of saltmarsh (81 ha) which contains high densities of crabs. The use of additional habitats at high tide would allow higher densities on the mudflats at low tide than could be supported by the prey base if all foraging was restricted to these mudflats. Similarly, Eurasian Oystercatchers have been found to rely heavily on supratidal habitats in addition to intertidal mudflats (Heppleston 1971), and the high density of shorebirds at the Berg River estuary was attributed in part to their utilisation of its extensive saltmarshes and nearby saltpans in addition to foraging on intertidal mudflats (Velásquez & Hockey 1992).

SUMMARY

1. Approximately 65% of Grey Plovers at the Zwartkops estuary, South Africa, defended feeding territories throughout the austral summer. Territories were established during the arrival period (September), once the foraging densities of Grey Plovers exceeded 4.6 birds per hectare. Territories ranged in size from 490 to 2800 m^2.

2. Average territory size decreased over the season and was significantly and inversely related to the total number of Grey Plovers on the estuary, rather than to resource patterns. Individual variation in territory size was inversely related to resource density.

3. Territorial encounter frequency decreased from September to March, probably due to neighbour familiarity, and was also reduced by avoidance behaviour. The frequency of aggressive encounters and the time spent in territory defence was significantly higher for owners of smaller territories.

4. The owners of large territories spent significantly more time foraging during the low tide period than did owners of small territories. However, energy intake rates were negatively correlated with territory size, with the result that that total low tide intake was approximately equal, irrespective of territory size.

5. Nonterritorial Grey Plovers foraged at higher densities than territorial birds. These birds achieved a decreasing proportion of the energy intake rate of territorial birds over the season, and may have had to depart later on northward migration.

INTRODUCTION

Many migratory shorebirds defend feeding territories on their nonbreeding grounds (Myers, Connors & Pitelka 1979a). Although the study of territoriality has become well established in recent years (Carpenter 1987a), the factors which govern territoriality in waders during the nonbreeding season are still poorly understood. Detailed investigation of this behaviour will contribute not only to the study of nonbreeding territoriality, but also to answering broader questions related to shorebird foraging ecology, competition and migration.

Territorial behaviour is widely reported amongst nonbreeding shorebirds, but relatively few detailed studies have been carried out (Hamilton 1959, Johnson, Johnson & Bruner 1981, Myers, Connors & Pitelka 1979b, 1981, Dugan 1982, Townshend 1979, 1985, Townshend, Dugan & Pienkowski 1984). Findings to date have been highly variable, with respect to the temporal and spatial scales of territoriality, as well as the extent to which territorial behaviour is prevalent in a population. Accumulated knowledge of the variability between and particularly within species under different conditions will facilitate identification of the proximate factors governing territorial behaviour (Myers *et al.* 1979a). Dynamic studies of variability in territorial behaviour in time are particularly valuable as they allow analysis of the behavioural plasticity of individuals in response to changing conditions. Furthermore, investigation of the relative energetic consequences of territorial and nonterritorial behaviour to individuals is required in order to understand the behavioural dichotomies within populations.

Grey Plovers have been reported to be territorial throughout the range of latitudes that they occupy during the nonbreeding season, e.g. England (Townshend 1979), Portugal (F. Moreira, pers. comm.), New Jersey (Burger, Hahn & Chase 1979), California (Myers *et al.* 1979a), Mauritius (pers. obs.), South Africa (this study) and Argentina (Myers & Myers 1979). This study examines the dynamics of Grey Plover territorial behaviour in a South African estuary over the nonbreeding season and addresses the following questions:

1. What controls territory size?
2. What influences aggressive behaviour?
3. How do territorial individuals differ in foraging behaviour and success?
4. What causes the behavioural dichotomy in an area where some birds are territorial and others are not, and are nonterritorial birds at an energetic disadvantage?

STUDY AREA AND METHODS

The study was carried out on the Zwartkops estuary, South Africa. The estuary and prey characteristics are described in detail in Chapter 1.

The study area was visited at approximately two-monthly intervals from February 1990 to March 1991, and in March 1993. Detailed observations were carried out on a study area of 1.45 ha within the 'Main' mudflat area (Fig. 2.1), where 25 unobtrusive coloured stakes were positioned at 20m intervals to form a grid of 80 x 80m. Additional observations were made on the intertidal mudflats of an adjacent 'creek' (3 ha) and 'island' (3.5 ha; Fig. 2.1).

Territorial boundaries and behaviour

Individual Grey Plovers were identified on the basis of plumage characteristics. During the arrival and premigratory periods, they varied considerably in the extent and patterning of breeding plumage, and were individually ranked by the degree of breeding plumage, from full breeding to full nonbreeding plumage.

To establish the boundaries of the birds' territories, the position of each bird on the study area was plotted in relation to the grid. These plots were made at approximately 20 - minute intervals over the low tide period for five days, so that more than 30 plots were made during each visit. A second observer timed and plotted all aggressive encounters that occurred on the study area throughout the low tide period. By combining these data, it was possible to demarcate the area occupied by each bird and to confirm the area boundaries from the positions of territorial encounters.

During March 1991, 34 plots were made at 10 minute intervals. The direction of movements of all neighbouring pairs of birds were analysed to test whether their movements were random with respect to one another. If the vector lines joining two consecutive plots for a pair were within 45° of one another, they were considered to be 'parallel'. It was assumed that if the movements of birds were random with respect to neighbours' movements, then the percentage of 'parallel' movements should be 25%.

Estimates of prey densities on the study area were obtained by counting the entrances of prawn burrows in 0.25m^2 quadrats at 20m intervals. From November 1990, sampling intensity was increased to 10m intervals. Each *Upogebia* burrow has two entrances, but more than one individual may be present in the burrow (MacNae 1957). Consequently, the number of entrances per m^2 was used as an index of prey density.

Numbers, densities and foraging behaviour and success

The methods used to calculate densities, foraging time, behaviour and energy intake

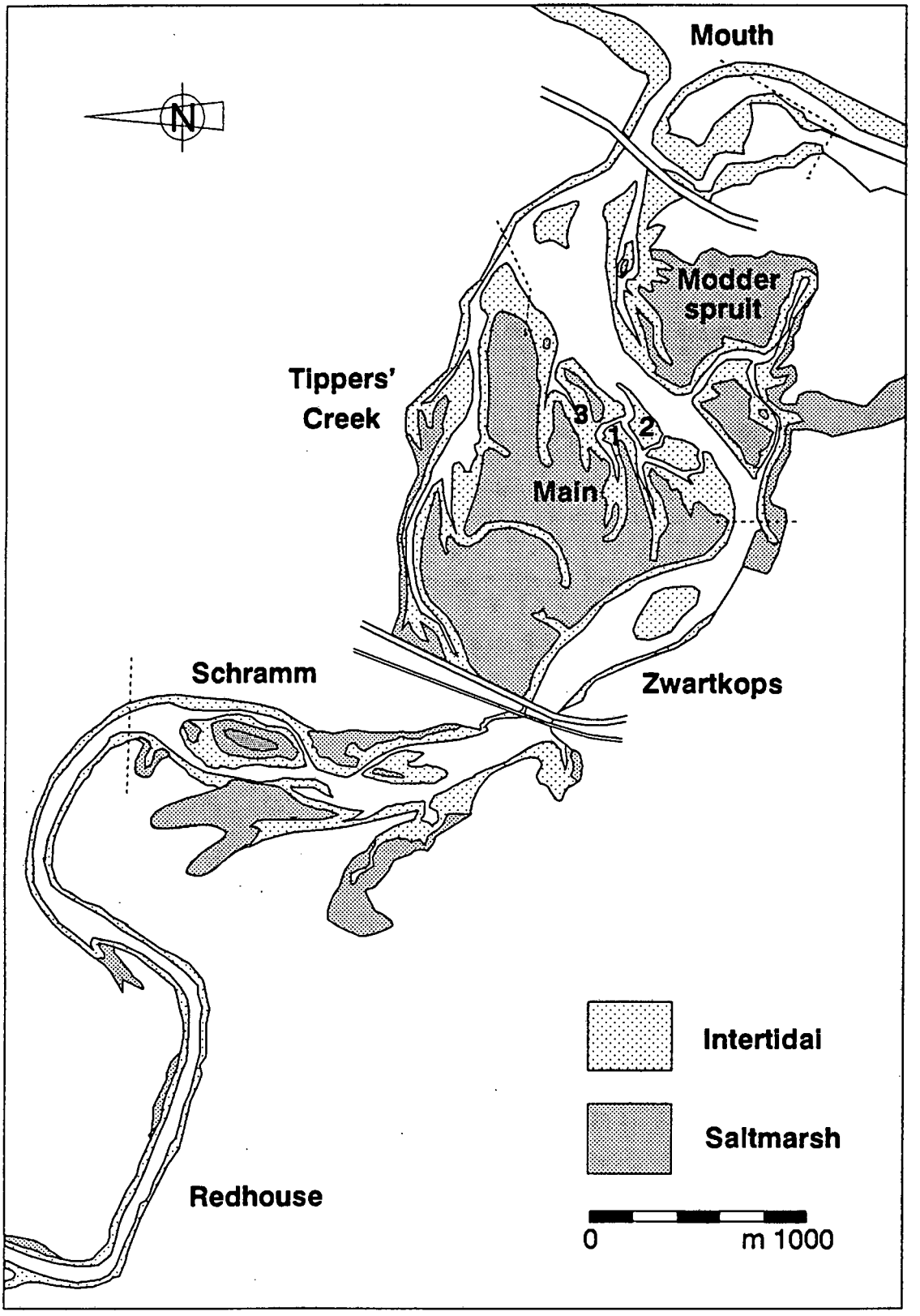


Figure 2.1. Map of the Zwartkops estuary showing the seven intertidal regions surveyed for Grey Plovers, and the study area (1), and adjacent 'island' (2) and 'creek' (3).

rates are described in Chapter 1. An additional 678 minutes of focal observations were made on nonterritorial birds, and 1 625 minutes were made on territorial birds in March 1993. Whenever possible, the identities of the birds were recorded during observations.

In addition, in March 1991 and March 1993, detailed studies were made of the time budgets of all territory holders on the study area. The activity of each individual was recorded at 5 minute intervals over three and seven low tide periods in respective years, and all aggressive encounters were timed.

RESULTS

Seasonal development of territories

Fifteen Grey Plovers defended territories on the study area in March 1990 (Fig. 2.2a). The few Grey Plovers that overwintered at the estuary did not defend territories. They remained in flocks and showed little feeding-site fidelity. Numbers on the 'Main' mudflats (incorporating the study area) increased rapidly during September (Fig. 2.3), but during the first half of the month numbers on the study area were low and variable, and no territorial behaviour was observed.

The first incidents of territorial behaviour were recorded during the second half of September, when the average density of Grey Plovers on the 'Main' mudflats was between 4.6 and 6.5 per hectare (Fig. 2.3). By 17 September, eight birds were defending territories on the study area (Fig. 2.2b). One of these, bird E, was immature. On 24 September, an intruder (bird I) arrived shortly after the residents, and despite repeated attacks from birds already holding territories, established a small territory (150m^2), which it expanded to 775m^2 the next day (Fig. 2.2c).

Two more birds had established territories on the study area by November (Fig. 2.2d), and a twelfth Grey Plover had established a territory by January 1991. No additional territories were established between January and March (Figs. 2.2e,f). In March 1991, birds C and J were captured and colour-ringed, after which bird J did not return to its territory for a week. During this time no new birds attempted to enter the vacated territory, but birds I and D expanded their territories into the area and negotiated a new boundary (Fig. 2.2f) until bird J returned.

In early September, before the establishment of territories, the density of birds on the territorial and nonterritorial study areas was equal (Fig. 2.4). After territories were established, the density on the territorial areas increased only very gradually through the summer, whereas densities on the adjacent nonterritorial 'island' increased rapidly before decreasing and stabilizing towards mid-summer. By March, densities on the nonterritorial area were about three times higher than on the territorial areas.

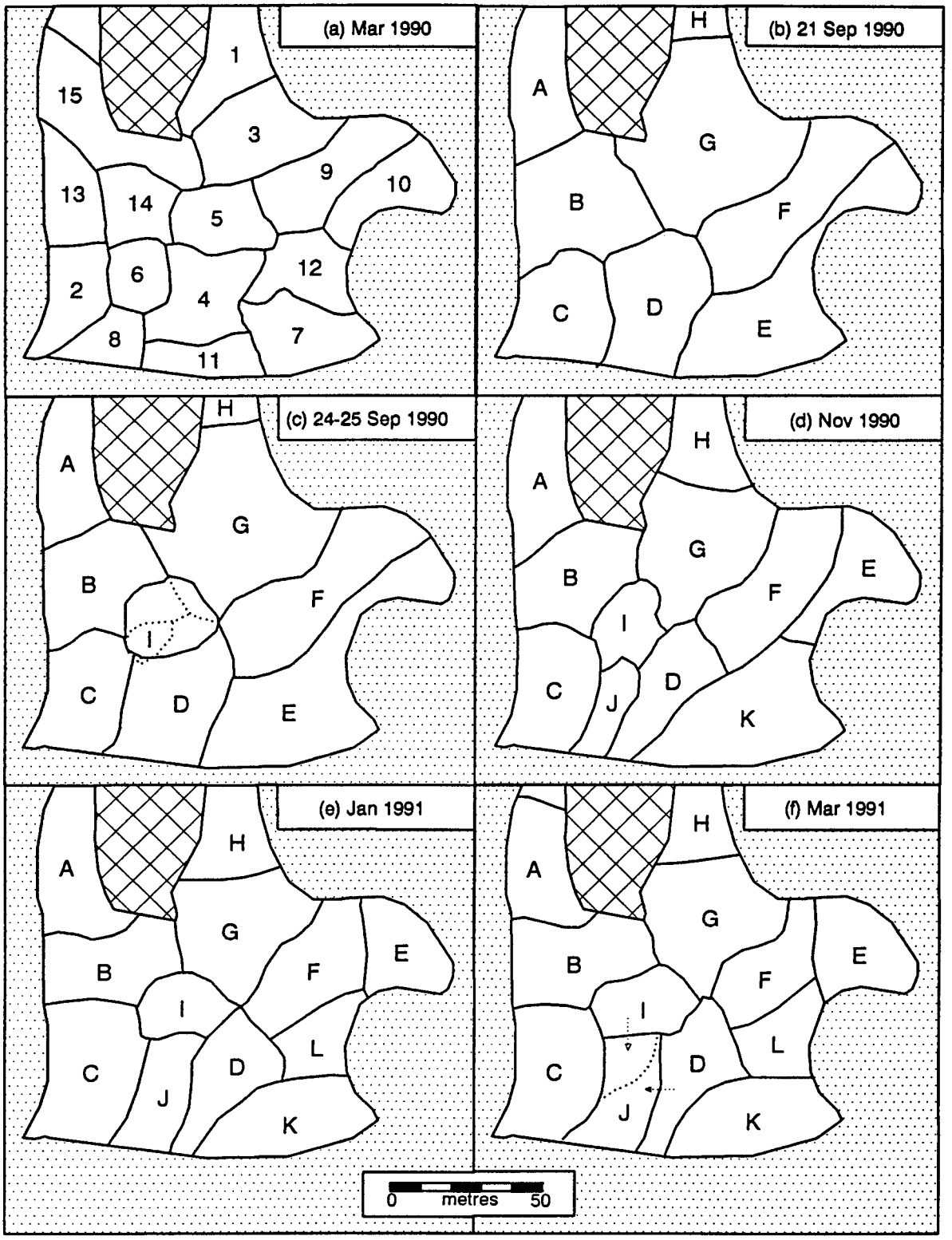


Figure 2.2. Seasonal changes in the layout of Grey Plover territories on the study area from March 1990 to March 1991. From September 1990, each individual is assigned a letter. The full extent of territory H is not shown. In (c) the dotted boundaries were mapped on 24 September, and the solid lines are boundaries on 25 September. In (f), the dotted line is the boundary that existed between birds I and D during the week of bird J's absence.

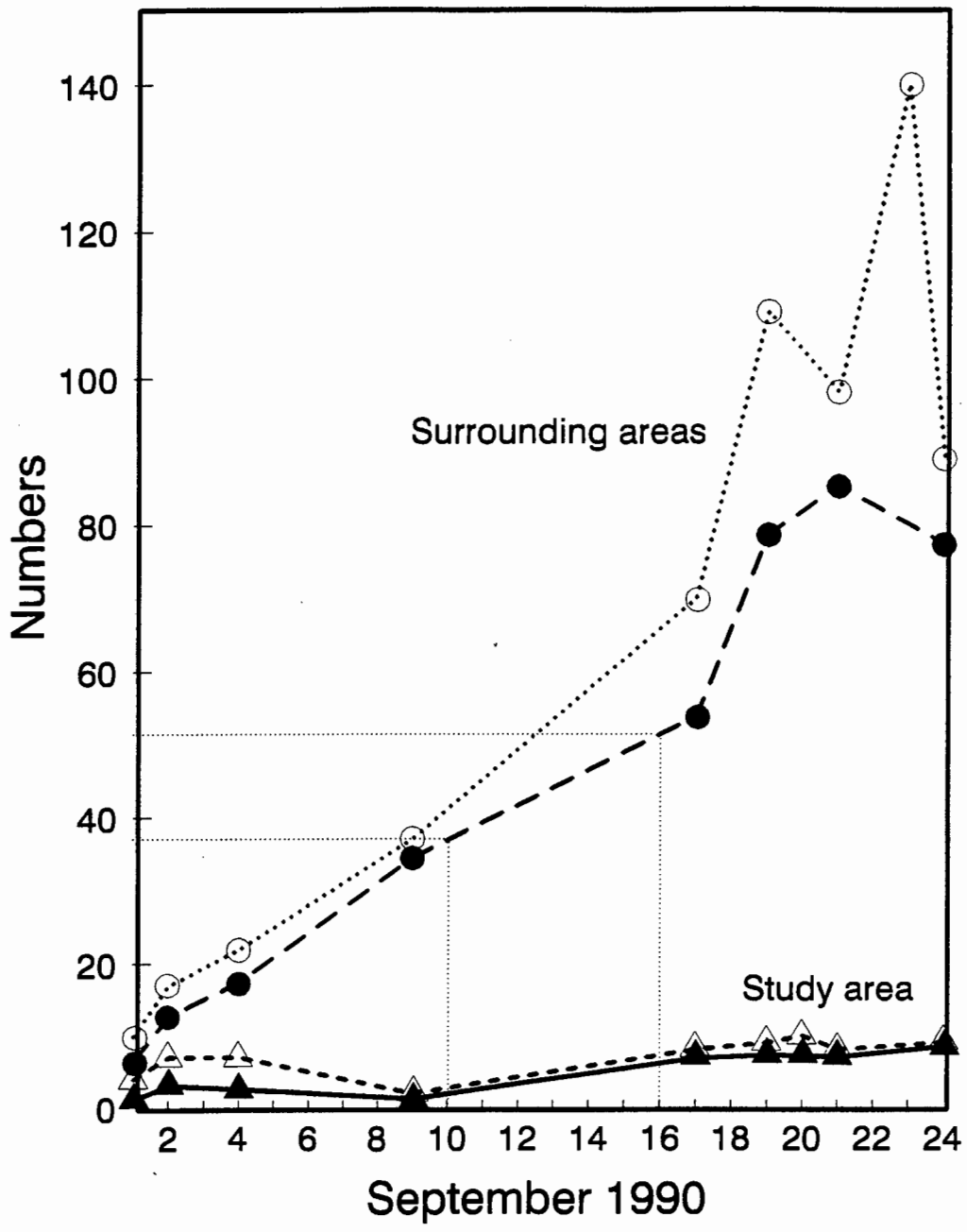


Figure 2.3. Average (solid symbols) and maximum (open symbols) numbers of Grey Plovers on the study area alone (1.45 ha; triangles) and including the surrounding area (total 8 ha; circles) during September. Boxes correspond to the dates before which birds were nonterritorial on the study area, and after which the study area was occupied entirely by territorial Grey Plovers.

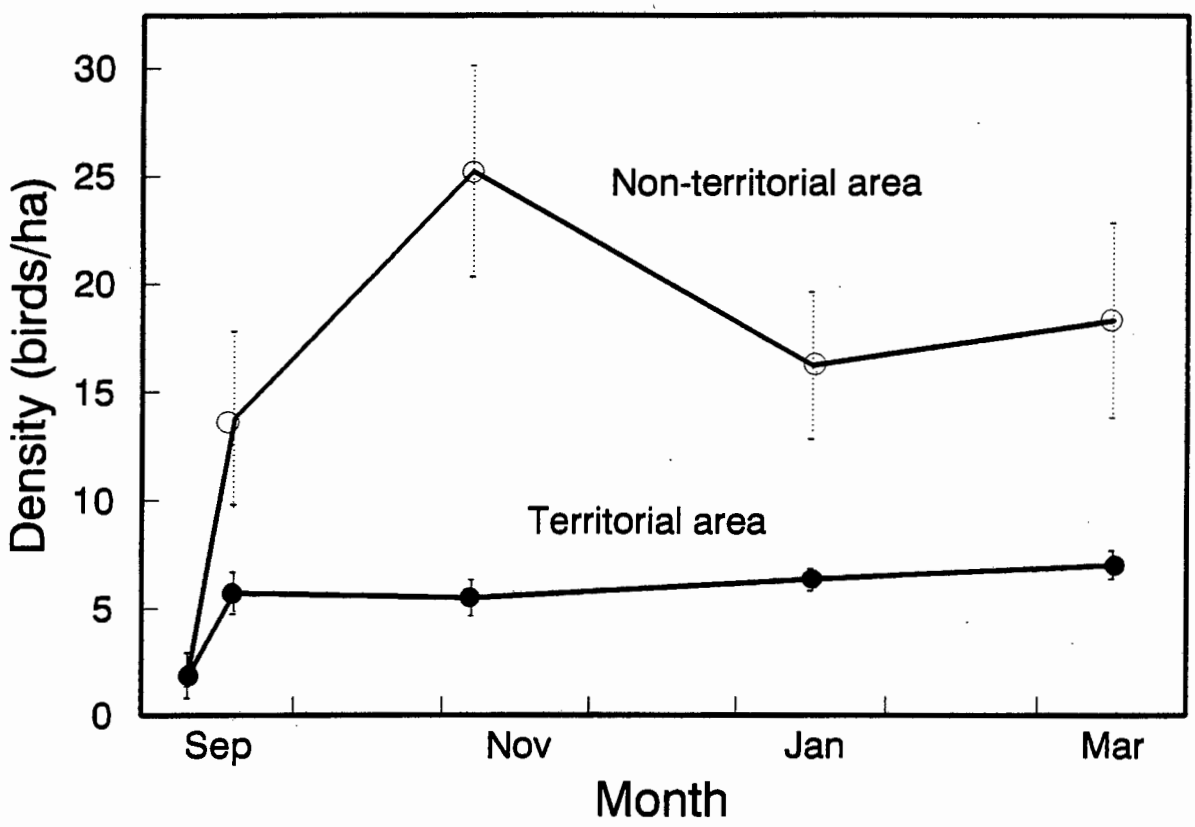


Figure 2.4. The density (mean ± S.D.) of Grey Plovers on the territorial study area (solid circles) and on the adjacent nonterritorial 'island' (open circles) during the summer.

Table 2.1. Seasonal variation in number of territories, average number of birds foraging (± S.D.) and aggressive encounter rates (from continuous monitoring) of Grey Plovers on the territorial study area, and aggressive encounter rates (from focal animal observations) on the nonterritorial 'island'.

Month	Territorial area				Nonterritorial area
	Number of territories	Average no. foraging	Hours of observation	Encounters per bird per hour	Encounters per bird per hour
Mar 1990	15	9.9 (± 3.8)	8	1.04	no data
May*	0	6.5 (± 5.2)	7	0.14	no data
Jul	0	0.4 (± 0.4)	8.5	0.00	no data
Sep1	0	2.2 (± 1.3)	4.5	0.61	7.89
Sep2	8	4.0 (± 2.0)	10	1.25	no data
Sep3	9	4.0 (± 1.8)	7.5	2.53	7.69
Nov	11	6.3 (± 2.5)	7	2.11	no data
Jan 1991	12	7.8 (± 2.6)	9.5	1.29	8.39
Mar	12	8.9 (± 2.6)	11.5	1.09	3.55

* Observations in May were made on the adjacent creek (3 ha), because no birds were present on the study area.

Aggression and spacing behaviour

Territorial encounters were usually initiated when one territory holder noticed a foraging neighbour approaching the territory boundary. The behavioural components of territorial encounters were ritualized, and were similar to those described for most plovers (e.g. Myers *et al.* 1979a). Normally, the aggressor ran up to the encroaching neighbour in a head-down, tail-fanned posture. The pair then walked parallel to one another along the territory boundary, about 0.3 - 1 m apart, sometimes pacing a section of boundary back and forth several times. They moved forward alternately, and frequently performed displacement feeding behaviour (*sensu* Hinde 1970). Parallel walking was periodically interrupted by bouts of posturing, when the birds displayed by tail-fanning, wing-drooping, and low crouching or sitting postures. The average duration of these encounters was 3.5 ± 3.2 (S.D.) minutes (n = 117), ranging from 0.2 to 19 minutes. There was no significant difference in the duration of encounters between November, January and March (Kruskal-Wallis One-way ANOVA, $H_{35,43,39} = 3.4$).

Very few aggressive encounters occurred amongst the few immature Grey Plovers that remained over winter (May & July, Table 2.1). At the beginning of September, aggression was still nonterritorial. Nonterritorial encounters were only of a

few seconds' duration, and did not involve the lengthy rituals of territorial encounters. The aggression rate doubled in mid-September, when the first eight territory holders were present, and the average number of Grey Plovers foraging on the area was doubled. With the arrival of the ninth territory holder later in September, the average encounter rate doubled again. However, 18 of the 38 encounters recorded involved the new bird, and the high encounter frequency was a temporary situation reflecting territory establishment rather than territory maintenance. Encounter rates remained high in November, but decreased thereafter, despite an increase in the average number of birds foraging on the area. Similar encounter rates were recorded in both years during the premigration period (March; Table 2.1).

The proportion of parallel foraging paths (within 45°) between neighbouring birds was significantly negatively correlated with their average distance apart (n = 17 pairs, r = -0.52, $P < 0.05$, Fig. 2.5). Neighbouring birds which foraged, on average, more than 40m from one another, tended to move at random with respect to one another (i.e. the proportion of parallel movements was close to 25%). The correlation coefficient was low, however, probably because each bird interacted with more than one neighbour.

Territory size, prey abundance and population density

The study area was relatively flat, and as the area became exposed, individual Grey Plovers did not arrive until their territories were exposed or shallow enough to stand in, ie. there was no flexibility in territory boundaries in response to tidal level.

Territory size was significantly and inversely related to prawn-hole density during March 1990 (n = 15, r = -0.66, $P < 0.01$), November (n = 11, r = -0.68, $P < 0.05$) and March 1991 (n = 12, r = -0.60, $P < 0.05$; Fig. 2.6). The relationship was not significant in September (n = 9, r = -0.58, P = 0.10), due to one outlying point (Fig. 2.6), but without this point the relationship was significant (n = 8, r = -0.80, $P < 0.05$). Nevertheless, the number of burrows defended per territory increased significantly with territory size during March 1990 (r = 0.76, $P < 0.01$), September (r = 0.75, $P < 0.05$) and November (r = 0.84, $P < 0.01$), but the slight increase in March 1991 was not significant (r = 0.14; Fig. 2.7).

Average territory size decreased from September 1991 to March 1992, as the number of territories on the study area increased from 9 to 12. The change in mean territory size over the season was not related to a change in prey abundance (burrow density) or to the seasonal trend in prey availability (number of prawns surfacing per unit area per low tide period, Martin 1991; Fig. 2.8). Mean territory size in different months was significantly negatively correlated with the total number of Grey Plovers on the estuary (Fig. 2.9).

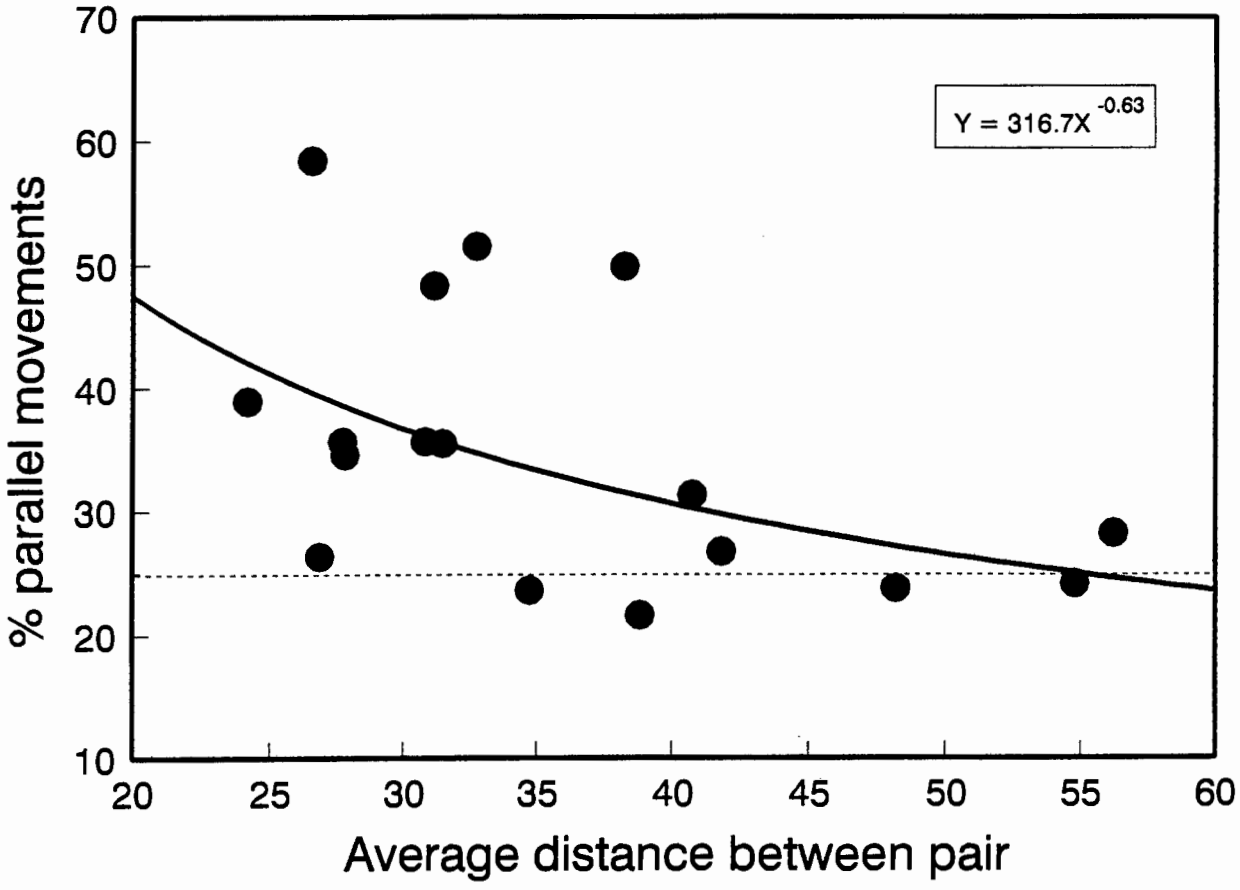


Figure 2.5. Percentage of movements of neighbouring pairs of territory holders which are parallel (within 45°) in relation to their average distance apart.

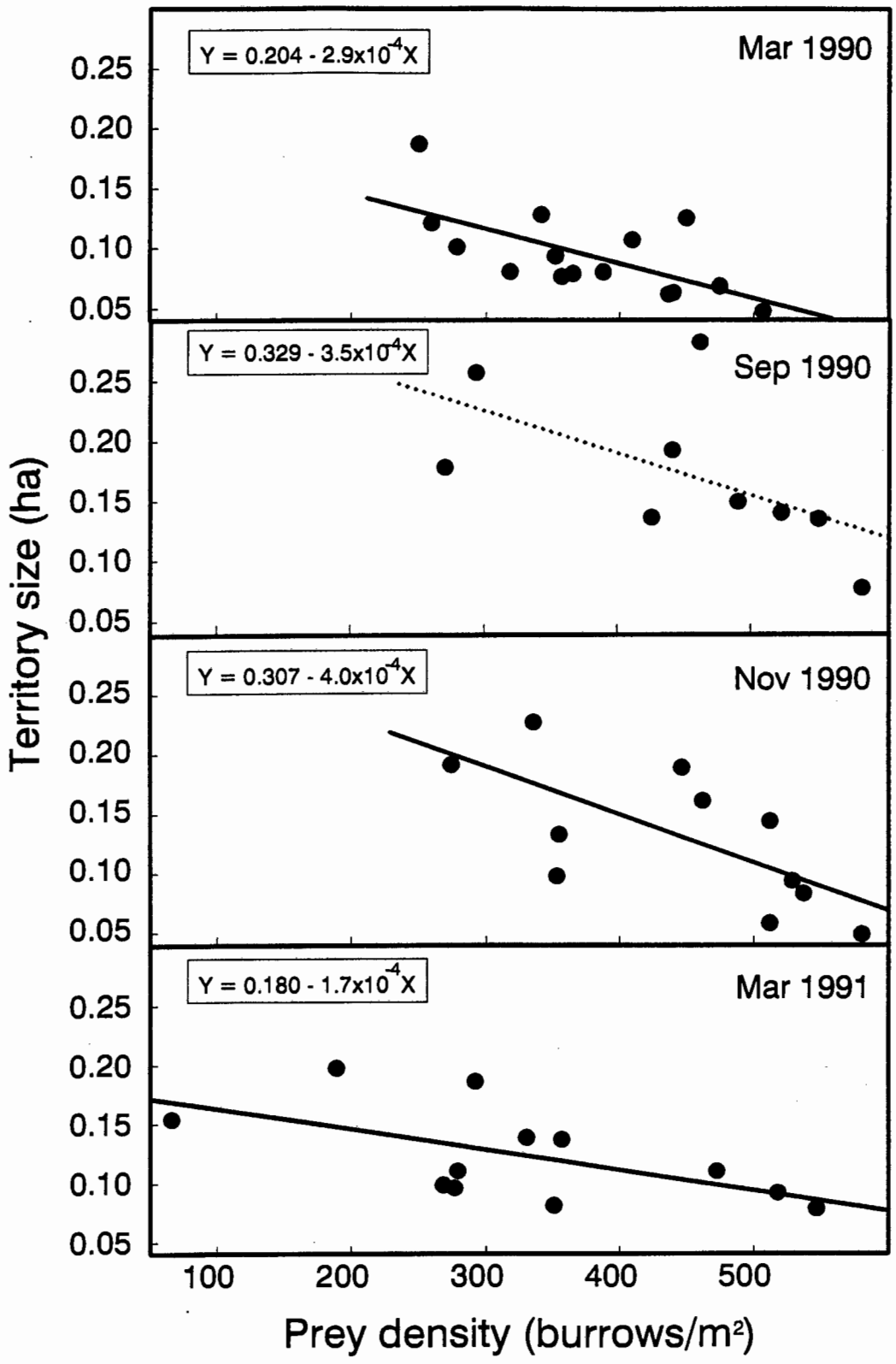


Figure 2.6. The relationship between Grey Plover territory size and the density of prawn burrows in different months.

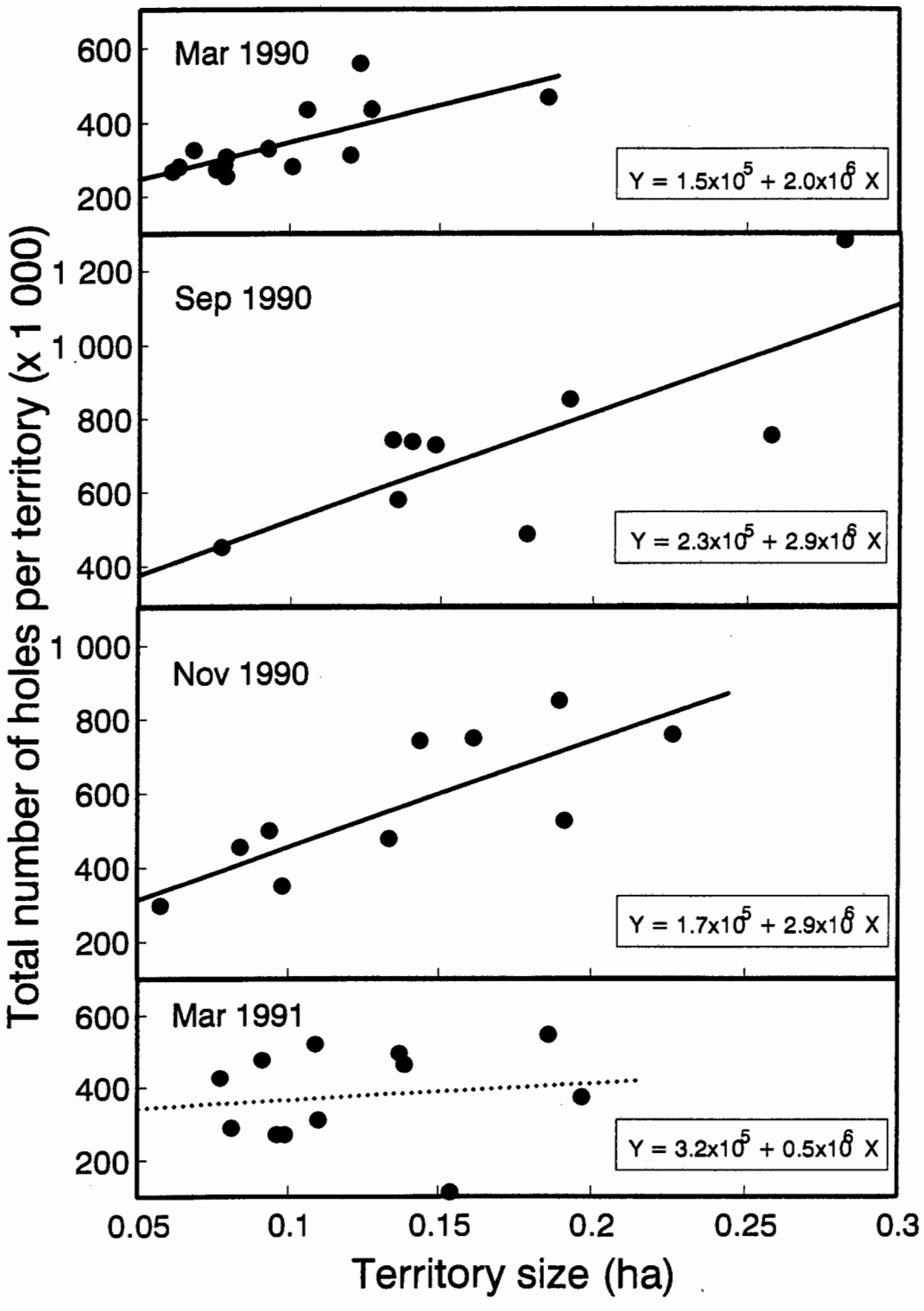


Figure 2.7. The number of prawn burrows defended in relation to territory size of Grey Plovers in different months.

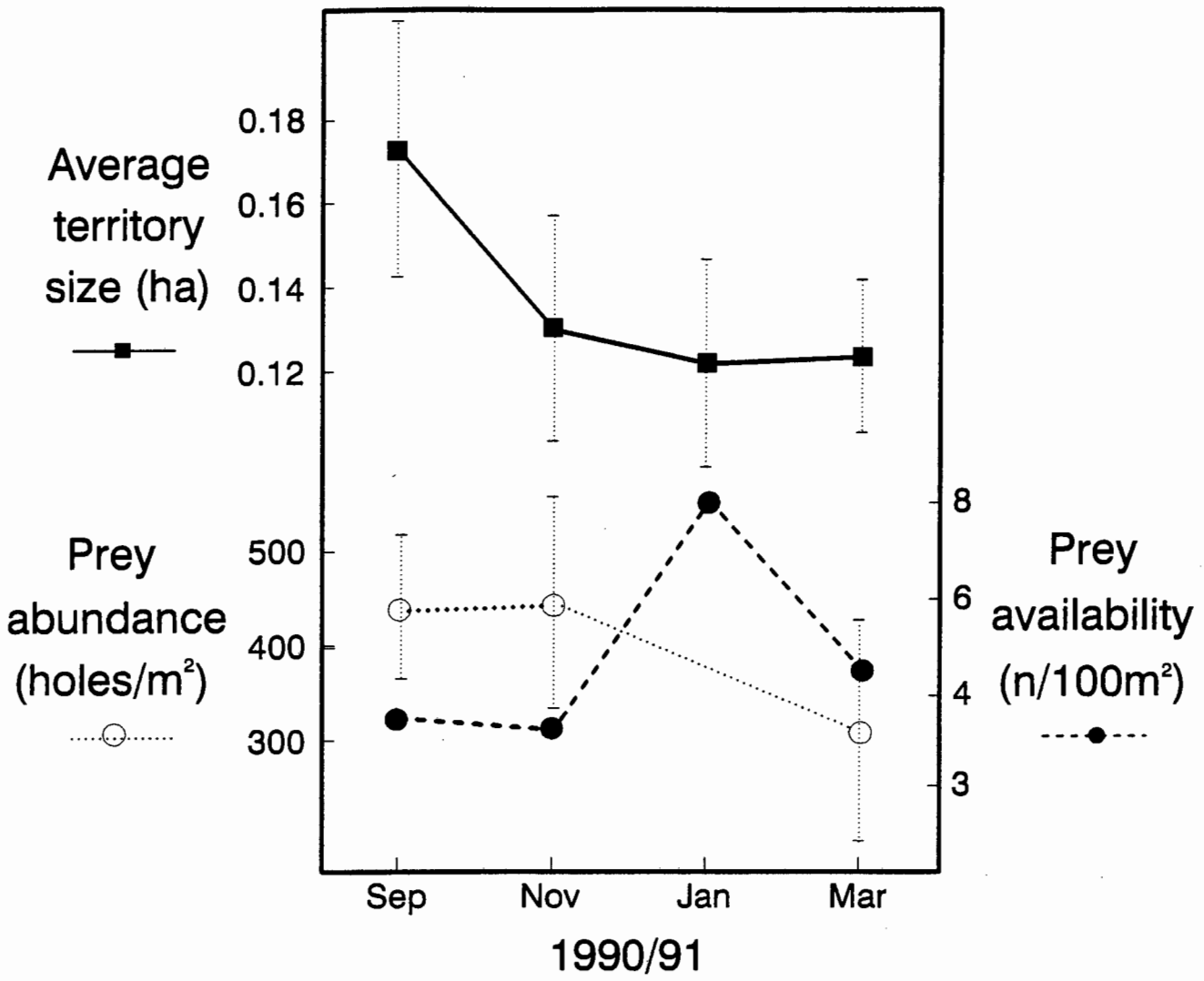


Figure 2.8. Seasonal trends in mean territory size (± S.D.), prey abundance (± S.D.; burrows/m^2) and prey availability (number of prawns surfacing per $100m^2$ per low tide period, Martin 1991). Prey abundance was not measured in January.

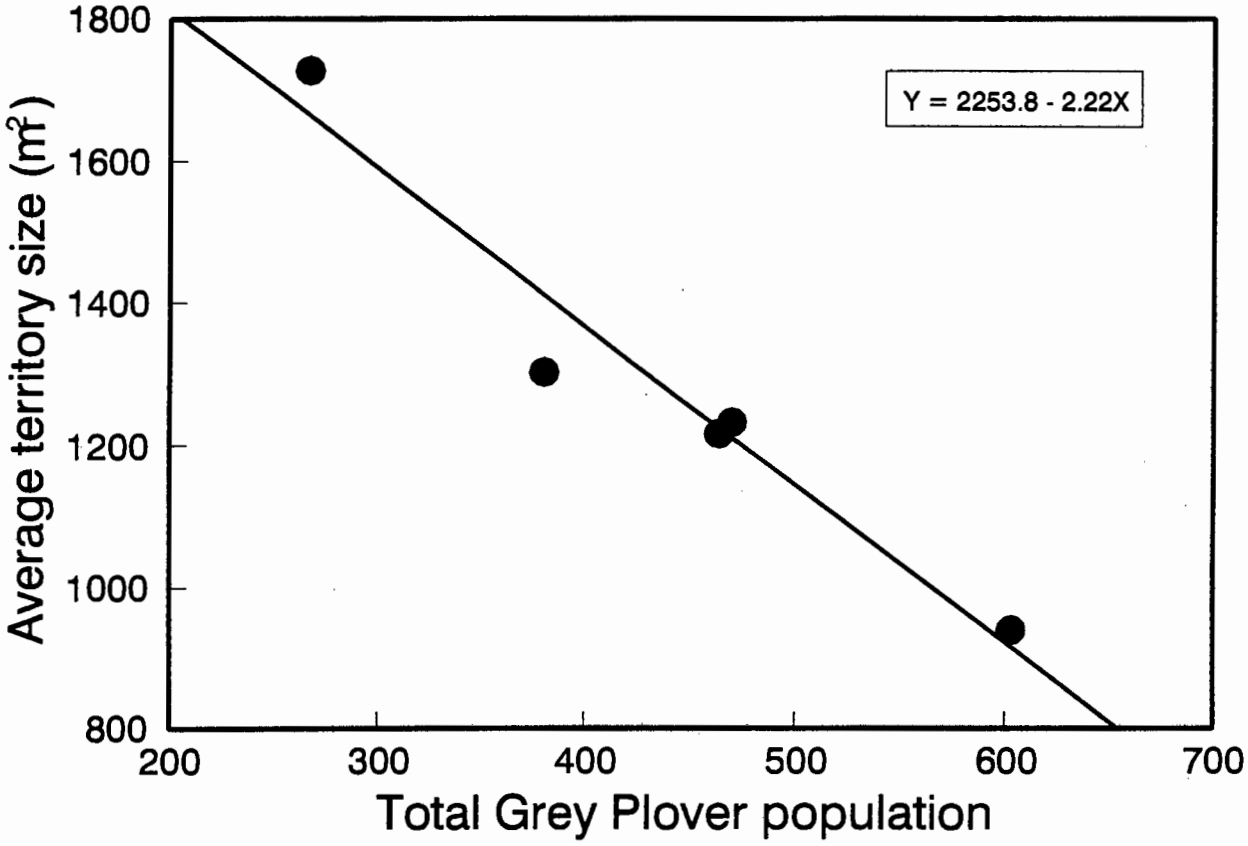


Figure 2.9. The relationship between average territory size (m^2) on the study area and the total number of Grey Plovers on the estuary.

Territory size, rank and foraging behaviour

During the premigration period (March 1990, 1991) there was no relationship between the extent of breeding plumage and territory size, energy intake rate, or the frequency of aggressive encounters (Spearman Rank Correlation). This suggests either that there is no hierarchy amongst territorial birds, or if there is, that it is not related to the timing of development of breeding plumage. Individuals changed their rank with respect to territory size from month to month, but there was still a significant association in individual rank among the months (Kendall's coefficient of concordance (W) = 20.16, $P < 0.01$). However, because individuals remain in the same area, and patterns of relative burrow density were fairly constant from month to month, this association need not be linked to a social hierarchy. Moreover, there was no significant month to month association in individual rank in terms of the number of burrows defended (W = 13.44, n.s.), which suggests a lack of hierarchial order.

There was a significant inverse relationship between territory size and the frequency of aggressive encounters in March 1990 (n = 15, r = -0.72, $P < 0.005$) and March 1991 (n = 12, r = -0.60, $P < 0.05$; Fig. 2.10), but this relationship was not significant in September, November or January. Detailed individual time budgets recorded in March 1991 also revealed a significant inverse relationship between territory size and the percentage of each territory holder's foraging (including aggression) time spent in aggressive defense of the territory (n = 12, r = -0.65, $P < 0.05$; Fig. 2.11).

In addition, these time budgets showed that for all birds on the study area during March 1991, except bird E which usually foraged for part of the day on an adjacent mudflat, the average total foraging time per bird per low tide period was significantly positively correlated with territory size (n = 11, r = 0.75, $P < 0.01$; Fig. 2.12).

A case study of seven territorial individuals

Seven birds (named A to G in descending order of territory size) were studied in detail for seven days in March 1993. Similar relationships were found to those in previous seasons, but in some cases there were exceptions. Territory size was closely and inversely related to prawn burrow density, except in the case of bird A which had a high burrow density and a large territory (n = 6, r = 0.95, $P < 0.01$; Fig. 2.13a). The total number of burrows defended per territory did not increase significantly with territory size in this case (n = 7, r = 0.65; Fig. 2.13b), and excluding bird A, the coefficient of variation in territory content (S.D./mean) was only 0.11. Aggression rate (encounters per hour) was inversely related to territory size (n = 6, r = -0.92, $P < 0.01$; Fig. 2.14), except for bird B, which had repeated encounters with a neighbour

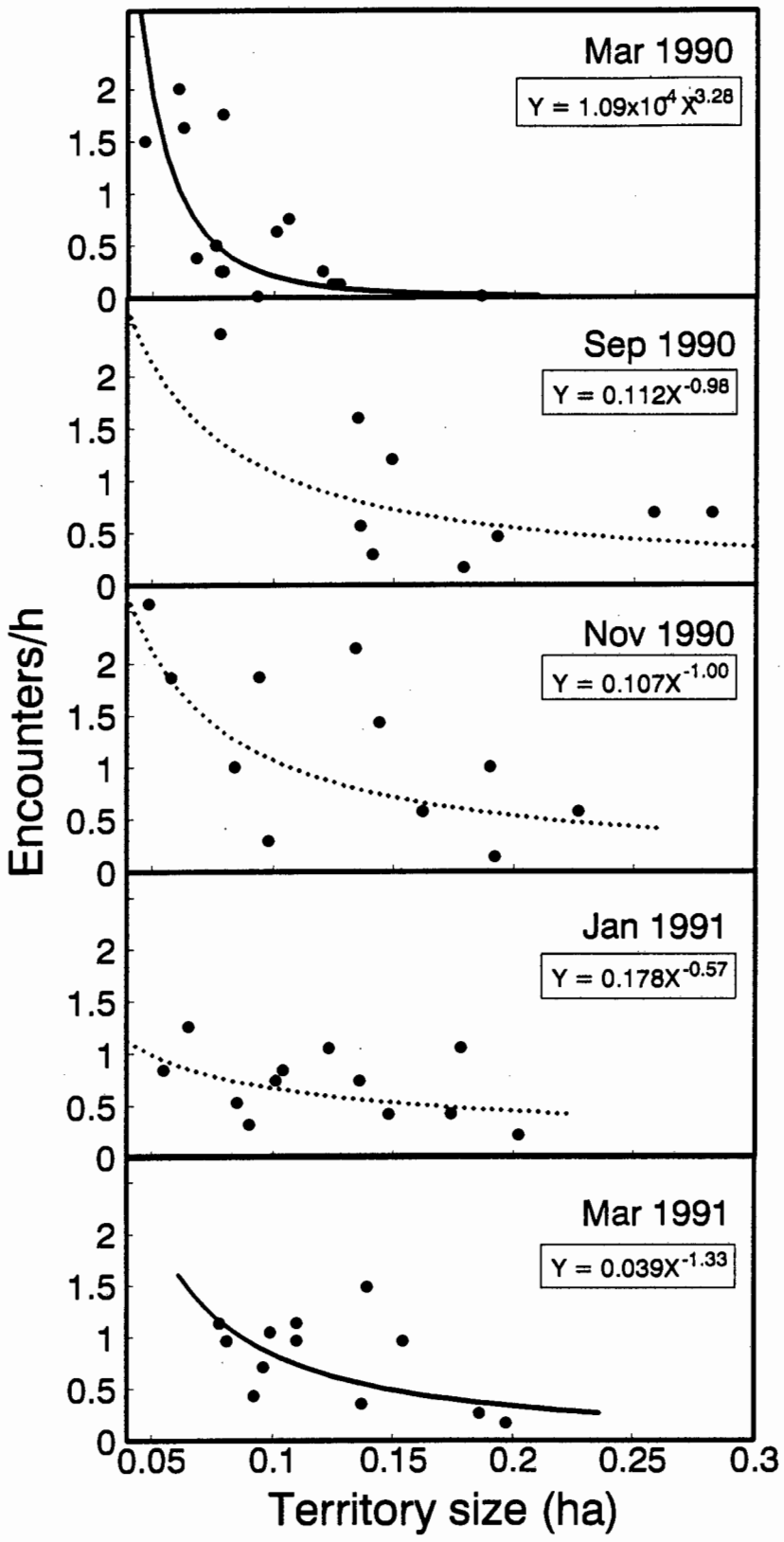


Figure 2.10. The number of aggressive encounters per hour of territory holders in relation to their territory size different months.

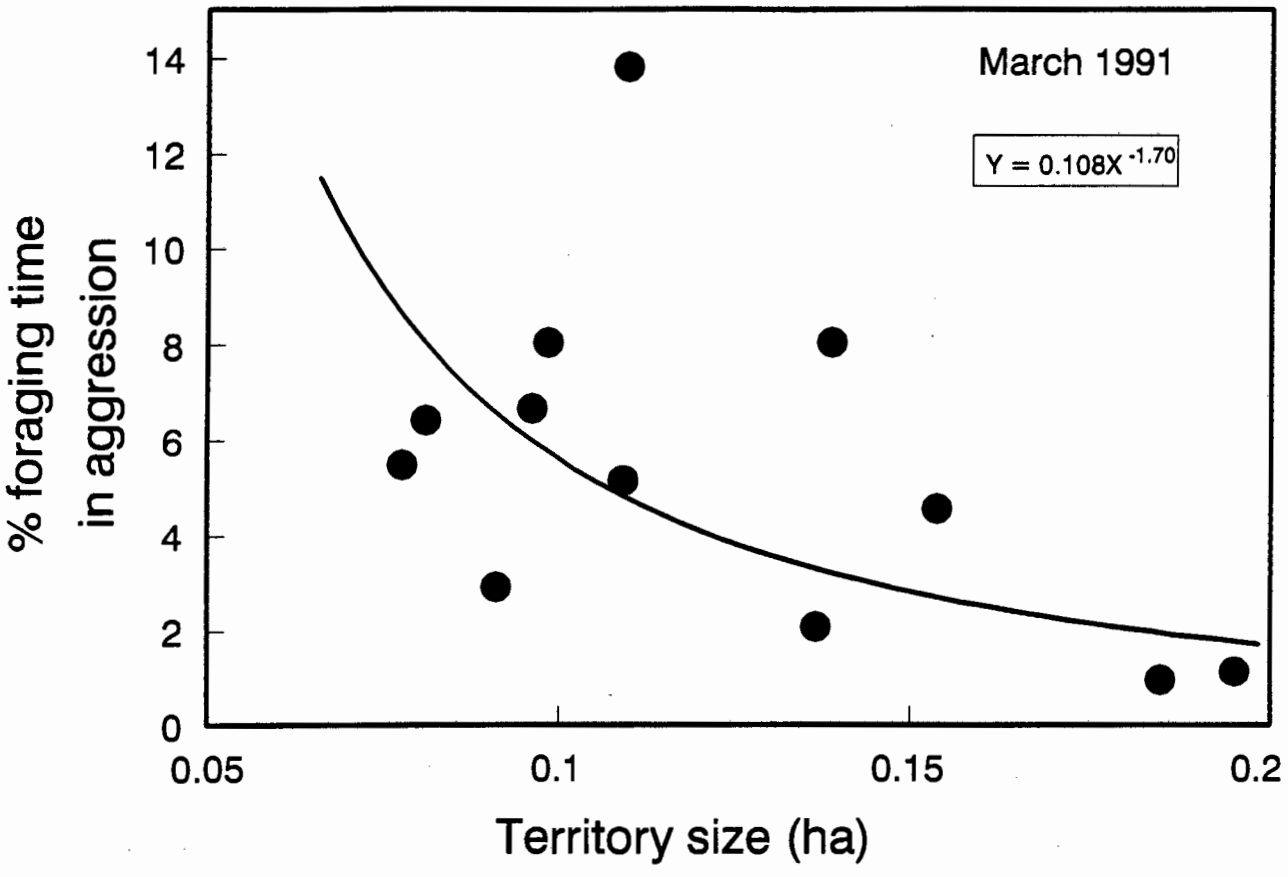


Figure 2.11. Percentage of foraging time (including aggression) spent in aggressive encounters by territory holders in relation to their territory size in March 1991.

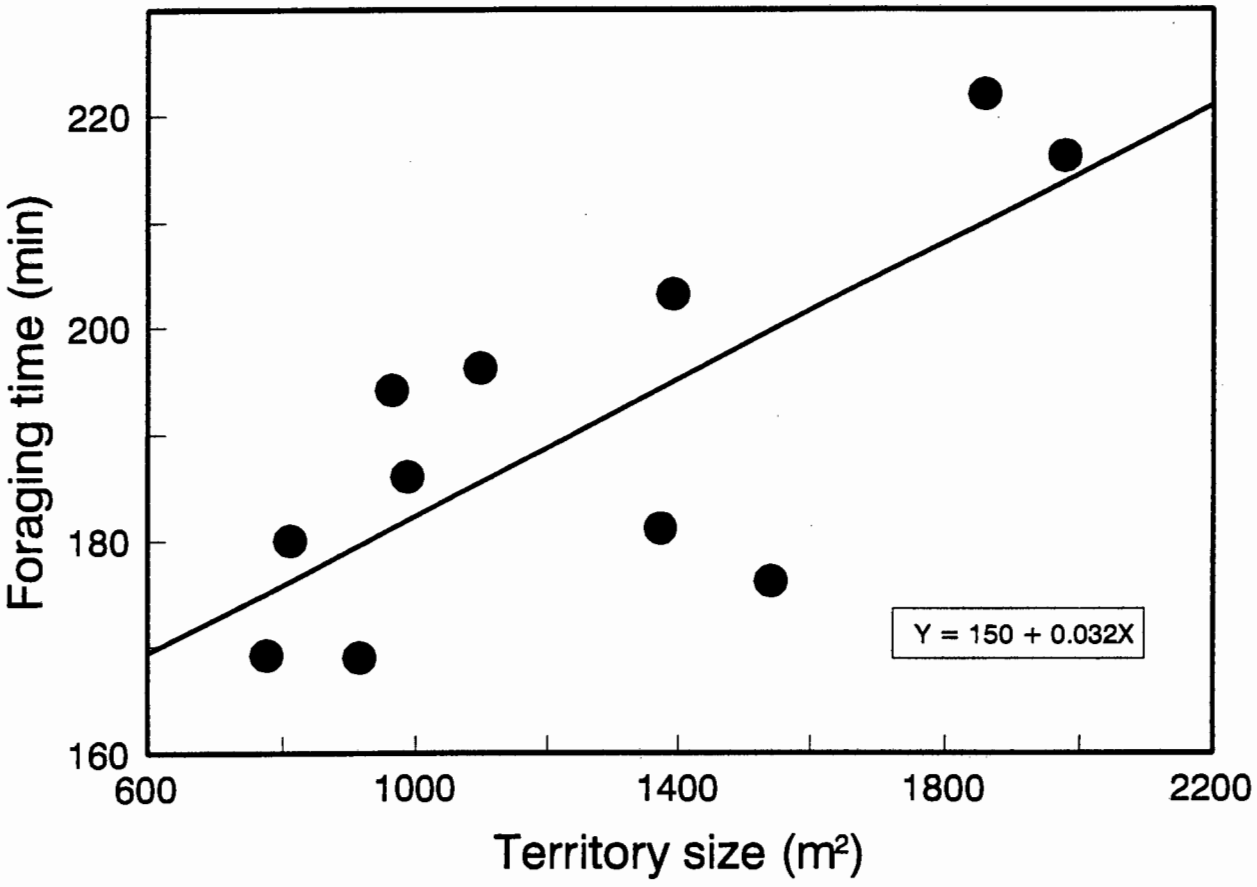


Figure 2.12. Average total time spent foraging per low tide period by Grey Plovers in relation to territory size during March 1991.

Table 2.2. Individual differences in the average daily low tide energy intake (kJ, ± S.D.), and in the percentage contribution of different prey types to energy intake of the seven birds studied during March 1993. Birds are listed in descending order of territory size.

Bird	Average daily intake (kJ)	% energetic contribution of prey			
		Prawns	Crabs	Polychaetes	Other
A	216.5 ± 29.9	68.2	25.9	0.1	5.8
B	156.9 ± 11.3	64.1	14.1	17.9	3.8
C	210.2 ± 20.5	81.9	8.9	8.9	0.4
D	203.6 ± 17.0	74.5	21.5	0.4	3.6
E	205.5 ± 15.2	73.4	26.2	0.4	0
F	214.3 ± 20.7	57.5	41.9	0.6	0
G	222.1 ± 22.9	78.7	15.7	1.6	3.9

on a small territory (not a focal bird), as was the percentage of foraging (including aggression) time spent in aggression ($n = 6$, $r = 0.86$, $P < 0.05$). Foraging time was significantly related to territory size ($n = 7$, $r = 0.92$, $P < 0.01$; Fig. 2.14).

In addition, net energy intake rate was negatively correlated with territory size ($n = 7$ $r = -0.81$, $P < 0.05$; Fig. 2.14), although bird B had a very low intake rate. Thus bird B's mean total low tide intake (157 kJ) was significantly lower than the other birds, whose mean total intake ranged from 204 - 222 kJ, and were not significantly different from one another (One-way ANOVA, $F_{6, 42} = 7.97$, $P < 0.01$; Tukey test). Total intake per low tide period was not related to territory size ($n = 7$, $r = -0.52$, n.s.; Table 2.2).

On average, 71.5% of net energy intake was gained from prawns, 22.5% from crabs, and 3.6% from polychaetes. However, the proportions varied between individuals (Table 2.2): birds B and C gained 18% and 9% of their energy from polychaetes whilst having the lowest energy gain from crabs, and B also had the lowest intake from prawns. Birds F, E and A had the highest proportion of energy gained from crabs, and G and C had the highest proportion of energy intake from prawns (Table 2.2). Neither the number of prawns captured per unit time nor their total energy content was related to territory size or prawn hole density, but mean prawn size taken by each individual was significantly correlated with burrow density ($n = 7$, $r = 0.79$, $P < 0.05$).

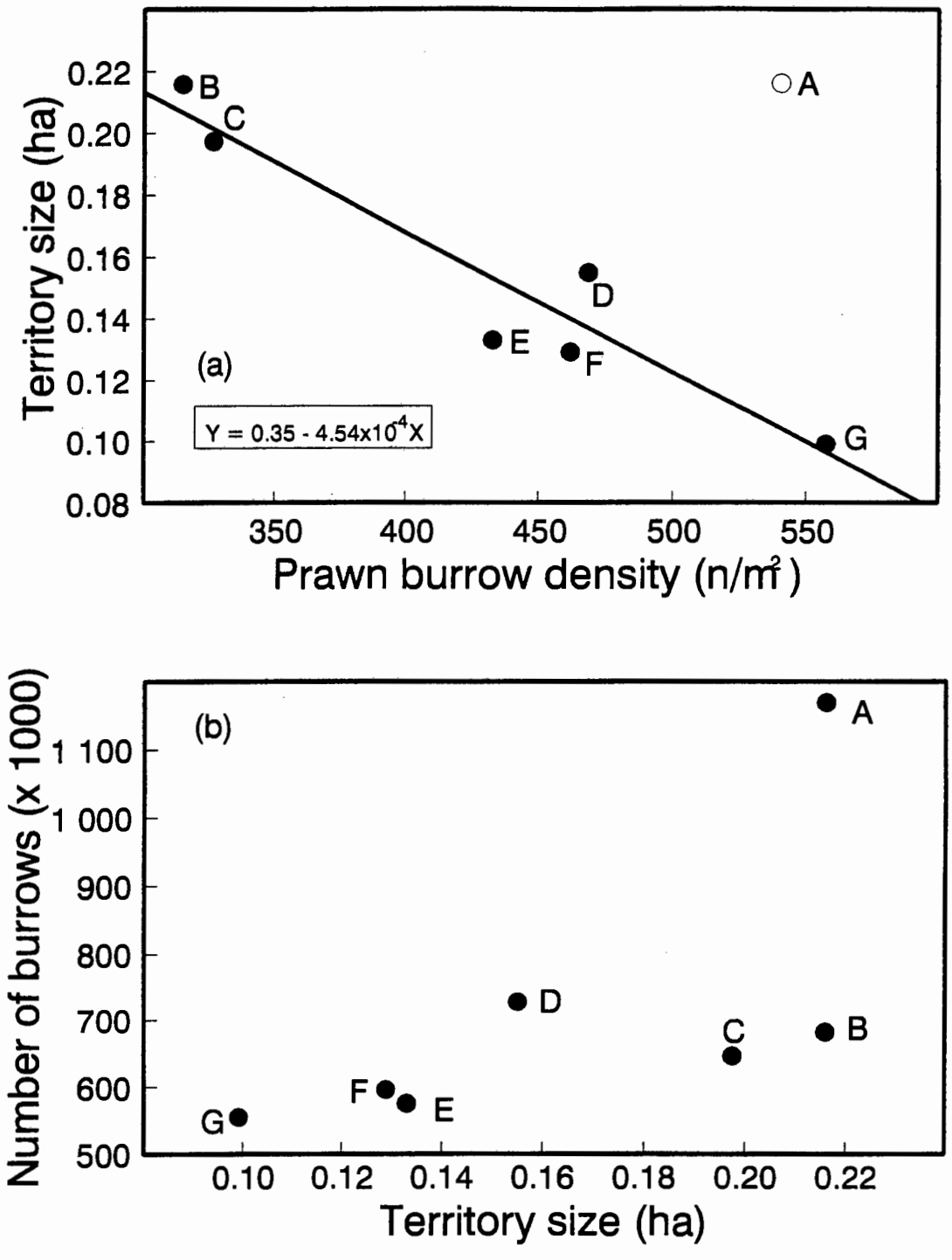


Figure 2.13. (a) The relationship between territory size and prawn burrow density of seven individuals in March 1993. Point A is not included in the regression. (b) The number of prawn burrows defended by each of the territory holders in relation to territory size.

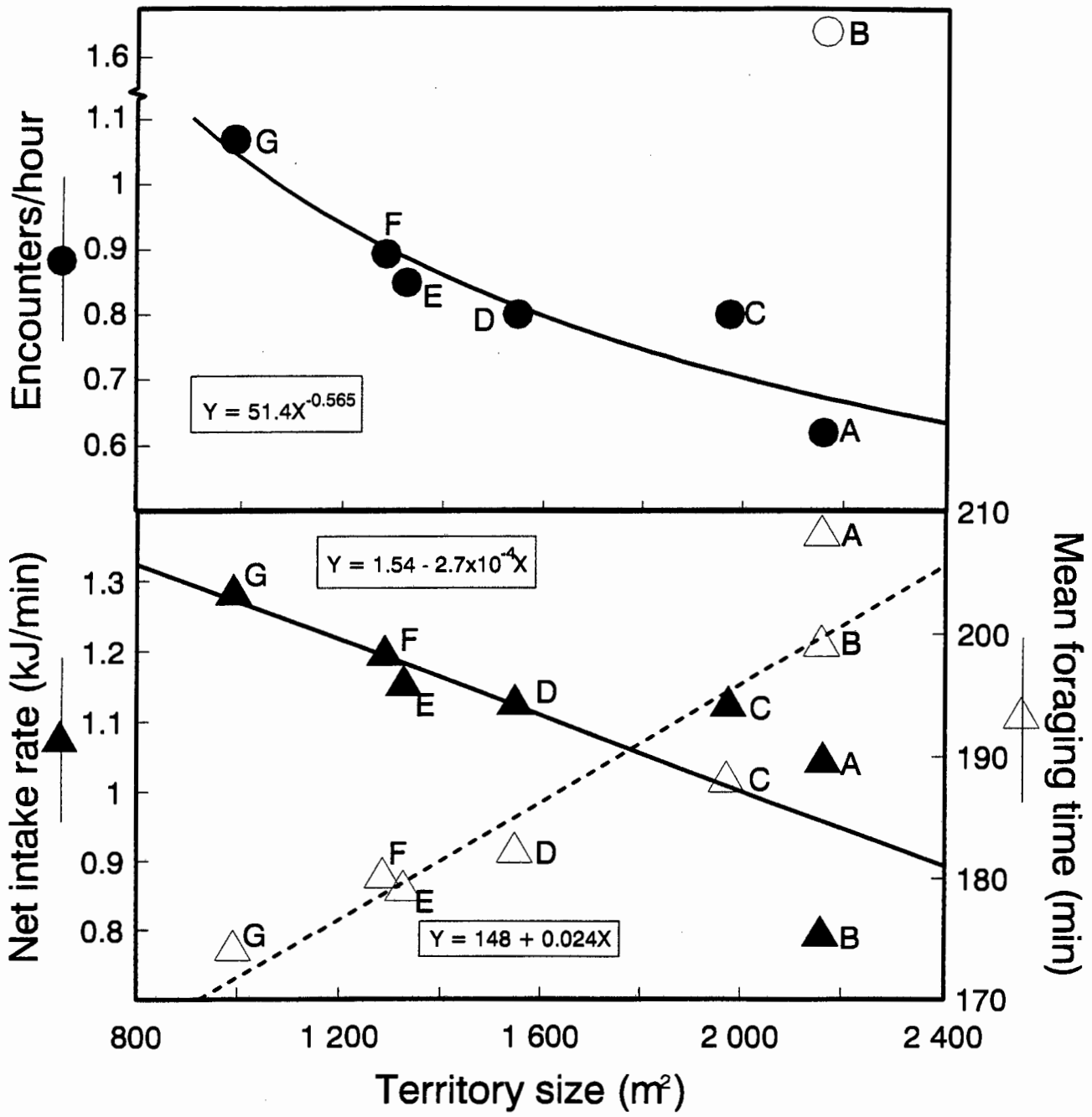


Figure 2.14. Encounter rate, net energy intake rate and mean low tide foraging time of seven individuals in March 1991. Individuals (A-G) are the same as in Fig. 12.

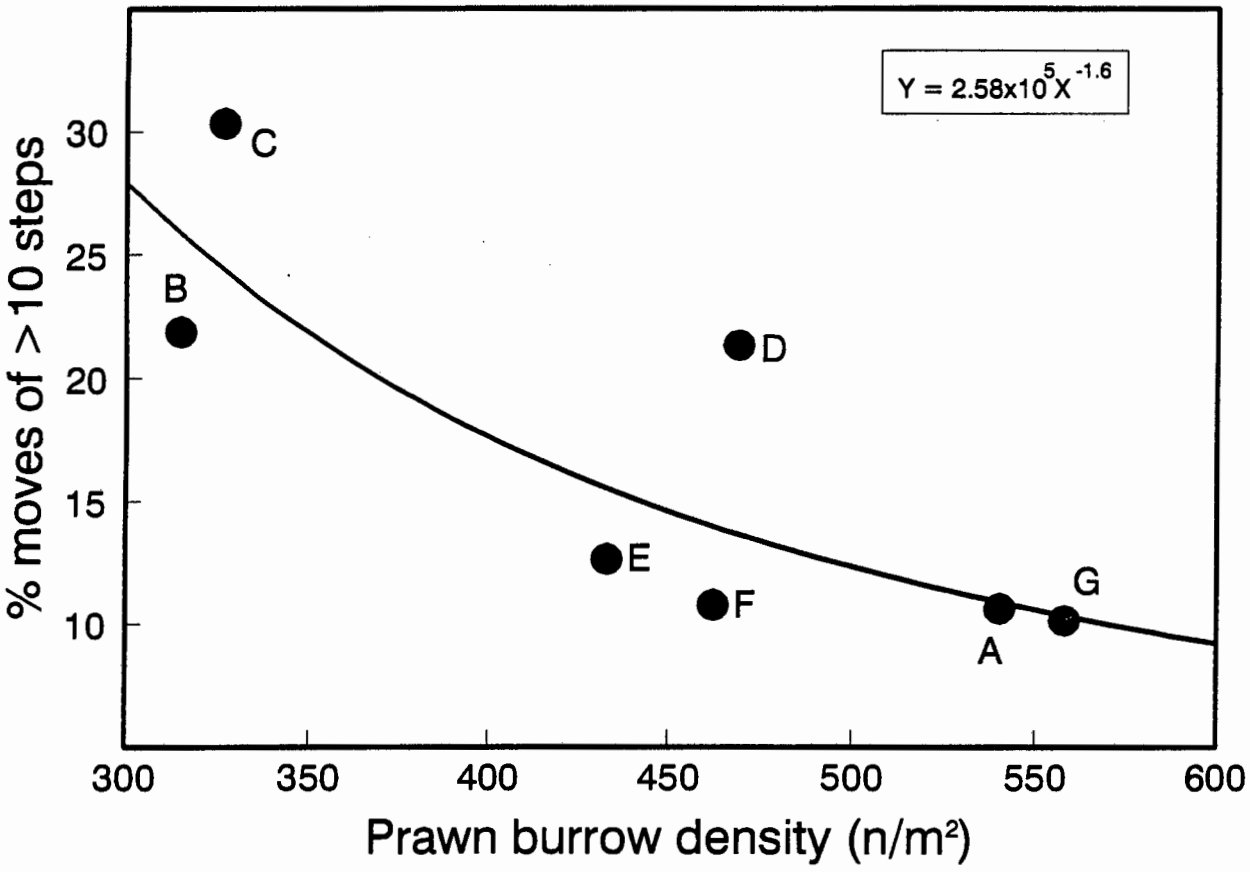


Figure 2.15. Percentage of foraging moves of 10 or more steps for each of seven individuals in relation to prawn burrow density of their territories.

Table 2.3. Average (± S.D.) net energy intake rate ($kJ.min^{-1}$) per bird, time spent foraging and total net energy intake (kJ) during the daytime low tide period by territorial and nonterritorial Grey Plovers, and the proportion of total low tide intake of nonterritorial birds relative to territorial birds (NT/T). Sample sizes (*n*) are numbers of birds.

	Territorial				Nonterritorial				
Month	*n*	Intake rate ($kJ.min^{-1}$)	Foraging time (min)	Total intake (kJ)	*n*	Intake rate ($kJ.min^{-1}$)	Foraging time (min)	Total intake (kJ)	NT/T
Sep1	9	1.44 (0.68)	182	262	10	1.15 (0.90)	225	259	0.99
Sep3	8	1.86 (0.53)	190	353	6	1.17 (1.03)	228	267	0.76
Oct	6	1.61 (0.72)	209	336	15	0.91 (0.90)	226	206	0.61
Jan	9	1.20 (1.16)	157	188	171*	0.37*	176	65	0.35
Mar	9	1.16 (0.33)	207	240	11	0.30 (0.29)	391	117	0.49

* Individuals were not identified, thus intake rate is for the total sample; sample size is given in minutes.

Although all the birds had a modal move length of either 2 or 3 steps, the frequency distribution of number of steps per foraging move differed significantly between individuals ($X^2_{6,4} = 229.5$, $P < 0.01$), and the percentage of long moves (of 10 or more steps) was significantly inversely correlated with prawn burrow density ($n = 7$, $r = -0.82$, $P < 0.05$, Fig. 2.15). Bird D is an outlier in this relationship, and may have had a lower burrow density than sampled, as also suggested by the relationship of territory size to prawn burrow density. This relationship does however confirm the high burrow density of bird A's territory. Bird B took significantly more steps per minute (average = 58) than the other birds (range 42 - 48), amongst which there were no significant differences (One-way ANOVA $F_{6,1624}$, $P < 0.01$, Tukey test).

Nonterritorial Grey Plovers

During the summer, Grey Plovers were territorial over most of the estuary, but nonterritorial birds were always present in certain areas. In March 1991, 77 ha (muddy areas) were occupied by territorial Grey Plovers, 11 ha (of mixed sediment type) were used by nonterritorial Grey Plovers and the remaining 16 ha (mostly sandy) of the intertidal area of the estuary were not used by Grey Plovers at all. Although numbers

were variable, nonterritorial birds on the estuary tended to be present at highest densities on the 'island' within the 'Main' mudflats (Fig. 2.1). The numbers of Grey Plovers on the island at low tide in March 1991 ranged from 25 to 122 (average 52), suggesting that at least 26% (122/470) of the Grey Plovers on the estuary were nonterritorial. After estimating the proportion of birds that were territorial on each section of the estuary during a survey, I estimated that 65% of the total population was territorial.

Before the establishment of territories during the arrival period, the energy intake rate of Grey Plovers foraging on the 'island' was 75% of those foraging on the study area (Sep1, Table 2.3). This ratio remained unchanged after the initial establishment of territories (Sep3, Table 2.3), although there was an overall increase in intake rates during this period. Throughout the summer residence period there was an overall decrease in energy intake rates, and nonterritorial birds achieved an increasingly small proportion of the intake of territorial birds between mid-September and March (Table 2.3). From September to January, nonterritorial birds spent between 8 and 24% more time foraging than territorial birds. In March, they foraged for nearly twice as long (Table 2.3). Foraging times of all birds were particularly short in January, due to a period of very short tidal exposure caused by a low-pressure system. Nonterritorial birds had a higher frequency of aggressive encounters than territorial birds (Table 2.1), but average encounter duration (6.1 $\pm$ 12.0 (S.D.) s; n = 67) was much less than that of territorial encounters, with the result that they spent approximately one fifth (19 $\pm$ 13%) of the time in aggression per unit time foraging than did territorial birds.

DISCUSSION

Territory size

Most of the seasonal variation in average territory size of Grey Plovers at the Zwartkops estuary could be explained by changes in the population density of conspecifics rather than changes in food resources. Mean territory size decreased from September to March, but prawn burrow density (prey abundance) also decreased during this period (Fig. 2.8). Furthermore, assuming that seasonal trends in prawn availability do not differ from year to year, the changes in average territory size did not follow the patterns of prey availability reported by Martin (1991).

Average territory size on the study area was closely correlated with the total number of Grey Plovers on the estuary (Fig. 2.9). From January to March, when there was negligible further increase in the number of Grey Plovers on the estuary, the number and sizes of territories remained constant. During March 1990 and March 1991, when the total Grey Plover population differed by 22%, the study area held 2.5 and 2.6% of the population respectively. These factors indicate that the decrease in average territory size over the season can be explained solely by the increase in the Grey Plover population size. Krebs (1971) found a similar reduction in Great Tit *Parus major* territory size at high population density which could not be ascribed to a change in resource density.

Within the limitation on average territory size set by population density, there is individual variation in territory size. Many studies have reported an inverse relationship between territory size and resource density, such that the quantity of resources per territory remains approximately constant (e.g. Clarke 1970; Gass, Angehr & Centa 1976; Salomonsen & Bald 1977; Kodric-Brown & Brown 1978; Gass 1979; Seastedt & MacLean 1979). Furthermore, some animals change the size of their territories in response to changing resource levels (Gill & Wolf 1975; Kodric-Brown & Brown 1978; Gass 1979). These patterns support a resource-based model of territory size, whereby animals adjust the size of their territories in order to defend a certain quantity of resources. Although there were no significant differences in the number of burrows defended by Grey Plovers at the Zwartkops in relation to territory size in March 1991 and March 1993, the number of burrows defended increased significantly with territory size in other months, suggesting that prey availability decreased disproportionately in relation to burrow density in these months.

Theoretically, territory sizes fall in a range within which the benefits accrued exceed the costs of defence (Brown 1964). The increase in Grey Plover population density on the Zwartkops estuary during early summer caused an overall decrease in territory size by raising the costs of defence. Increased costs reduce the range of

resource quantities which are economically defendable (Kodric-Brown & Brown 1978), and accordingly, the ranges of Grey Plover territory sizes and of resource quantities defended decreased over the season. Within this framework, costs and benefits influence territory size on a local scale. At constant prey density, the costs of territoriality increase with territory size and at constant territory size defence costs increase with prey density. Benefits accrued increase with territory size to an asymptotic maximum, and in areas rich in prey resources, this asymptote will be reached at a relatively small territory size. There has been some discussion however, as to whether territory sizes, within the range of economic defendability, are altered to maintain some energetic optimum, e.g. the size which maximises net benefit (Davies 1978, MacLean & Seastedt 1979), minimizes costs (Pyke 1979) or maximises territory size (Myers *et al.* 1979b, 1981).

Myers *et al.* (1979b, 1981) found that the size of Sanderling *Calidris alba* territories was limited entirely by intruder pressure. Myers' (*op. cit.*) study birds were foraging in an area of unpredictable resources, and the birds apparently attempted to defend as large an area as possible. At the Zwartkops estuary, where the prey supply is relatively predictable, Grey Plover territory sizes were also controlled primarily by competitor density, and there was no evidence that these birds were not defending maximally-sized territories. In contrast, Pyke (1979) calculated that sunbirds defended the quantity of resources which minimised their costs rather than maximizing their net benefits. If Grey Plovers at the Zwartkops estuary adjust the size of their territories to minimise costs, territories would have been expected to approach their minimum size from the beginning of the season.

Figure 2.16 illustrates a model proposing equal net benefits for all territory holders. If the total energy gain is approximately equal for all territory holders, then for their net benefits to be equal, the costs involved should also be equal. However, although the birds in the richer areas at the Zwartkops estuary defended smaller territories, they experienced the highest levels of aggression, implying that the owners of larger, but poorer quality, territories were better off. This apparent anomaly can be resolved by taking into account the fact that the costs involved in holding territories do not solely comprise defence costs. Intake rates were lower in larger territories and these individuals had to forage for longer in order to meet their energy requirements (Figs. 2.12, 2.13b). This extra foraging time was longer than the extra time spent in aggression by small territory owners, but although territory defence involved walking more slowly than when foraging, and energy expenditure is correlated to walking speed (Fedak, Pinshow & Schmidt-Nielsen 1974), territory defence also involves the cost of having to move away from favoured foraging areas. Although these costs are difficult to quantify, it appears likely that all territory owners enjoy equal net benefits. This is

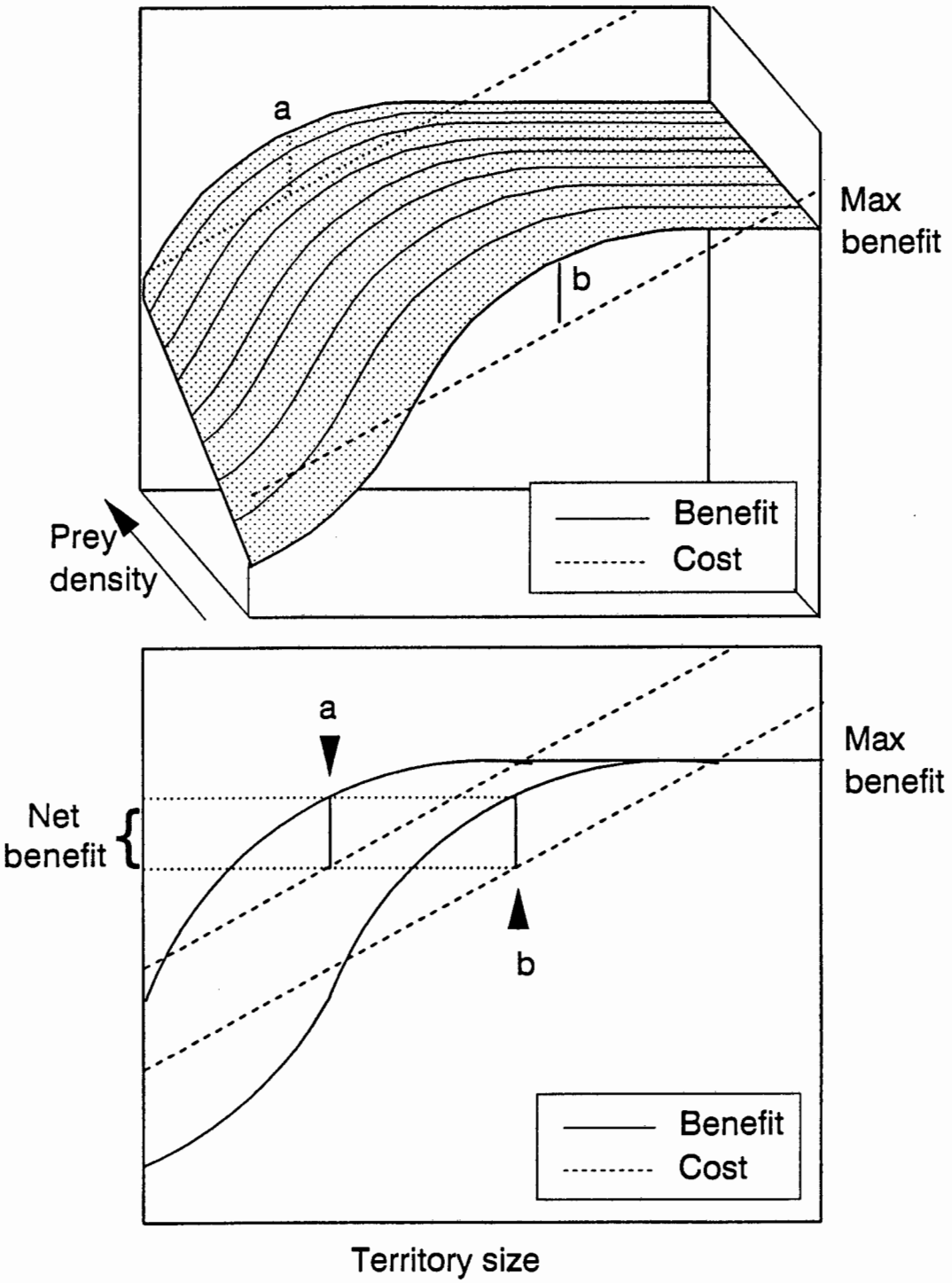


Figure 2.16. Three-dimensional diagram illustrating the relationships between resource density, energetic costs and benefits of territory defence, and territory size, and the range of territory sizes where net benefit > 0. The two-dimensional diagram illustrates that, with equal costs and benefits, territory owners on resource-poor and -rich areas achieve equal net benefits.

supported by the apparent lack of social hierarchy exhibited by the random ordering in individual territory content from month to month.

Aggressive and spacing behaviour

Despite being offset by lower foraging effort, the relatively high defence costs of small, resource-rich territories requires explanation. Territorial defence primarily involved border disputes with neighbours, rather than conflict with outside intruders. The higher-than-expected rates of encounters experienced by holders of small territories was probably because they were more likely to approach their territory boundaries whilst foraging and thus elicit an aggressive response from neighbours, rather than because of high resource density *per se*.

Encounter rates were highest at the beginning of the season and decreased thereafter. A similar pattern occurred in territorial American Golden Plovers *Pluvialis dominica* (Johnson, Johnson & Bruner 1981), as well as in Grey Plovers at the Tees estuary, England (Dugan 1980). Aggression between Grey Plovers at the Zwartkops estuary decreased during summer despite the increase in population density and the pressure to increase energy intake rates prior to migration. It appeared that neighbours contested their boundaries less often as they became familiar with one another. Although neighbours are important intruders in this and other territorial systems (Paton & Carpenter 1984; Smith & Ivins 1986) it has also been suggested that they are mutually beneficial in territorial defense (Getty 1987). I have observed neighbour co-operation in evicting an outside intruder, but outside intrusion was so rare on the study area that it was difficult to assess the importance of this behaviour. However, neighbour familiarity may be an important advantage of long-term territoriality, in allowing a gradual reduction in the costs of defence. By the premigratory period, when energy intake rates were lowest and foraging time increased (Table 2.3), the amount of time spent in aggression was very small. In this respect, Carpenter (1987b) interpreted territoriality as a form of sociality, suggesting that the reduction of defence costs in this manner allows animals to hold larger territories than would be the case if defence costs did not diminish with time.

Parallel-foraging behaviour probably also contributed to the lack of aggression between neighbours. There are two possible motivations for adopting a foraging path parallel to that of neighbours. It may serve to keep the neighbours in sight so they can be monitored with minimal effort (foraging visually allows birds to be aware of their neighbours with little extra vigilance effort), or it could result from mutual avoidance behaviour, in that approximately parallel foraging paths are less likely to converge than are random foraging paths.

Territory owners thus minimized defense costs by avoiding confrontation

through their foraging behaviour, by low-intensity ritualized territorial encounters, and by reducing encounter frequency through neighbour familiarity. The fact that there were no interstitial spaces between territories may partly explain the lack of intrusion by nonterritorial birds.

Territoriality: optional or optimal?

Brown (1969) identified three systems of breeding territoriality at the population level: in a level 1 situation, all individuals hold territories; in a level 2 situation, optimal territories are saturated and the remainder of the population occupy sub-optimal territories; and, in a level 3 situation, both optimal and sub-optimal territories are saturated, leaving a residual group of nonterritorial individuals. Most studies of shorebird territoriality on the nonbreeding grounds have found a pattern analagous to Brown's (*op cit*) level 3 situation (Hamilton 1959, Myers *et al.* 1979b, Johnson *et al.* 1981, Dugan 1982, Townshend *et al.* 1984), and there are no recorded instances where all individuals in a migrant shorebird population occupy territories during the nonbreeding season. There are three possible explanations for this behavioural dichotomy:

(a) different strategies are equally effective;

(b) one strategy is more successful and birds compete to employ it; or

(c) individual differences in competitive and foraging skills determine an individual's strategy, and an individual's optimal strategy may therefore change with age (Goss-Custard 1985).

Townshend *et al.* (1984) argued that short-term benefits of each strategy under contrasting conditions lead to equal advantage in the long term ((a) above). They suggested that territorial birds survive better during harsh years or periods because their food stocks are better conserved (see Dugan 1982). Nonterritorial birds, on the other hand, are better able to take advantage of supplementary food stocks that require mobility to obtain. Nonterritorial Grey Plovers at the Tees estuary forage on the nocturnally active *Nereis virens* away from their normal foraging areas at night (Dugan 1981, Townshend *et al.* 1984). At the Zwartkops estuary prey availability is not significantly different by day and night anywhere on the estuary (Martin 1991), and territorial birds occupied the richer areas both by day and night (Chapter 3). It is thus difficult to predict any situation in which nonterritorial birds may have an advantage over territorial birds at this estuary. The energy intake rates of territorial birds decreased over the season along with a decrease in territory size, but the energy intake rate of nonterritorial birds was increasingly lower than that of territorial birds as the season progressed. The nonterritorial birds may thus have experienced considerable difficulty in achieving sufficient premigratory weight gain. It is possible that territorial

individuals depart first, and nonterritorial birds move into the optimal areas, where they may be able to make up this deficit fairly quickly due to reduced competition. However, they may pay the price by arriving late at the breeding grounds. The different behaviours are thus clearly not equal in terms of reward.

According to explanation (b) above, all territorial space should be occupied by early arrivals, with later arrivals either being nonterritorial or ousting established territory owners. However, at the Zwartkops estuary, a proportion of the Grey Plover population was nonterritorial throughout the season. This suggests that certain individuals were unable to attain and retain territories (even when competition levels were low early in the season; explanation b), or did not attempt to establish territories due to some inferior characteristic (explanation c). Under (b), available territories are limiting, and under (c), they may or may not be limiting. There was clear potential for an increase in the number of territories, which was only realized later in the season. The rarity of intrusion by nonterritorial individuals, and the failure of any outsider to attempt to occupy the territory left vacant for a week during March 1991, suggests that territories are not limiting. Some Grey Plover territories at the Tees estuary are initially large and later reduced due to competition, but new territories are also established in previously uncolonised areas (Dugan 1980), suggesting a similar lack of territory limitation. These findings favour an explanation of territory establishment being dependent on individuals' competitive ability (c).

Although the relative sizes of territorial and nonterritorial Grey Plovers at the Zwartkops estuary is unknown, nonterritoriality was not restricted to juveniles, as during March 1991, 54% of territorial and 45% of nonterritorial Grey Plovers had started to develop adult breeding plumage. In addition, some juveniles defended territories at both the Zwartkops and the Tees estuaries (Townshend 1985). An individual's genetically determined body size is more likely to influence competitive ability, although age (and experience) may play a role. The fact that Grey Plovers at the Tees estuary tend to be consistent in their behaviour from their first year (Townshend 1985) supports this argument.

SUMMARY

1. During the premigratory period (March), Grey Plovers and Whimbrels at the Zwartkops estuary, South Africa, foraged throughout the nocturnal as well as the diurnal low tide period.

2. Although both species continued to forage visually at night, they exhibited behavioural changes to compensate for the reduced visibility. Both species foraged more slowly at night, taking fewer steps per minute, and Grey Plovers paused for longer to search for prey.

3. Prey items were sighted from shorter distances at night than during the day.

4. Energy intake rates did not differ significantly by day and night for either species, and both achieved over 40% of their daily low-tide period intake at night.

5. The energy intake rates and total daily intake of Grey Plovers, which fed exclusively on the study area, exceeded allometrically calculated values. However, total daily intake was similar to the daily requirement predicted from lean mass and the extra energy required for premigratory weight gain.

INTRODUCTION

The daily energy budgets of free-living waders can be estimated either from allometric equations (e.g. Bryant & Westerterp 1980, Kersten & Piersma 1987, Nagy 1987), or by direct field observation. At least 38% of the 110 species of intertidally-foraging waders (Hayman, Marchant & Prater 1986) have been reported to feed at night as well as during the day (e.g. Drinnan 1957, Smith & Evans 1973, Tree 1978, Alterogt & Davis 1980, Burger 1984, McNeil & Robert 1988, Zwarts, Blomert & Hupkes 1990b, McNeil 1991, Morrier & McNeil 1991, Velasquez, Kalejta & Hockey 1991, pers. obs.; Appendix 3.1) and it is certain that many, if not most, others do so. However, few field studies have included accurate observation of nocturnal activity budgets and energy intake rates in their calculations of daily energy budgets.

Observational studies of nocturnal foraging made to date have either estimated gross gain over entire tidal cycles, or have measured the rates of various foraging parameters (Appendix 3.2). Most of the former (e.g. Drinnan 1957, 1958a, Prater 1972, Hulscher 1974, 1976, Greenhalgh 1975, Hockey & Underhill 1984) were made using captive techniques, gut analysis or quantification of prey remains. These studies thus assumed either that experimental conditions approximate field conditions, or that all prey taken were accounted for when examining gut contents or prey remains in the foraging area. Studies which quantified foraging rates were mostly restricted to quantification of peck, probe and step rates or numerical intake rates of prey, and many studies were based on small sample sizes (e.g. Davidson 1968, Heppleston 1971, Greenhalgh 1975, Evans 1976, Sutherland 1982a,b, Pienkowski 1983, Swennen 1990, Martin 1991). These studies necessarily assumed that the ratios of diurnal and nocturnal foraging effort (peck or step rates) and energy gain were equal, or that the ratio of diurnal to nocturnal prey intake rates approximated the energy intake ratio, i.e. the same species and sizes of prey were taken by day and night. Only one study has quantified energy intake rates of waders at night (Zwarts & Dirksen 1990).

The aim of this study was to quantify the relationship between foraging behaviour, numerical and energy intake rates, and the total daily energy intake of Grey Plovers and Whimbrels during consecutive day and night tides. Specifically, the following key questions were addressed:

1. Do birds which are obligate visual foragers by day (Grey Plovers) or facultative visual/tactile foragers by day (Whimbrels) change their foraging behaviour at night, and can nocturnal energy intake rates be predicted on the basis of foraging rate?
2. How important is nocturnal foraging to the daily energy budget of these two species?

STUDY AREA AND METHODS

The study was carried out at the warm temperate Zwartkops estuary, South Africa during March 1991. The estuary and prey characteristics are described in Chapter 1.

Mudprawns at the estuary exhibit a peculiar (possibly parasite-induced) behaviour in that some individuals emerge from their burrows onto the mud surface at low tide (Martin 1991). This behaviour is most pronounced among the larger size-classes of prawns. Prawns on the surface vary seasonally in number, and are the major food source for most of the birds which feed intertidally on the estuary (Martin 1991, Chapter 1). There was no significant difference between the numbers of prawns surfacing during day and night tides (Wilcoxon's test, $T = 5.5$, $P > 0.1$; Table 3.1). Furthermore, the average size of prawns surfacing by day (carapace length 15.9 $\pm$ 5.4 (S.D.) mm, $n = 140$) and night (carapace 15.6 $\pm$ 4.5 mm, $n = 114$) does not differ significantly (t-test, $t = 0.43$, $P = 0.67$; Martin 1991). On this basis it was assumed that prawns were equally available by day and by night.

Observations were made on a mudbank of 1.5 ha, where both species had been observed intensively over the previous 12 months. Grey Plovers and Whimbrels foraged in this area by day and night and the mudbank was sufficiently small for all birds to be visible at all times. The study site was as far away as possible (1 km) from artificial light sources.

Daytime observations were made with Kowa TSN1 telescopes fitted with 20X wide-angle lenses. Night observations were made with a tripod-mounted HV7 x 200AT passive image-intensifier. This intensifier was fitted with a three-stage 25mm fibre-coupled tube and had an exceptionally high resolution of 0.35 to 0.50 mrad at 10^{-3} to 10^{-4} lux, i.e. the total light gain in the tube exceeded 35 000 times.

Each species was observed for two full day and night tides. Foraging time was calculated by means of activity scans and foraging behaviour and success were recorded in 608 and 348 1-min focal-animal observations for Grey Plovers and Whimbrels respectively. In both activity scans and focal observations, time spent in aggression was included as foraging time.

The numbers and activity (foraging or resting) of Grey Plovers and Whimbrels on the study area were recorded in half-hourly activity scans throughout each low tide period. As the proportion of juveniles in the population was low, Whimbrels were not separated by age class during activity scans.

The average time spent foraging (Ft, in minutes) by an individual bird was calculated as:

$$Ft = \Sigma t_{i..j} \, [I(Ft_i/Fmax)],$$

Table 3.1. Number of *Upogebia* prawns coming to the surface of a $400m^2$ plot during consecutive day and night low tide periods (A.P. Martin unpubl.).

	Site 1			Site 2	
Month	Day	Night	Month	Day	Night
Mar	9	10	Mar	40	26
Jun	0	6	Jul	2	1
Sep	18	8	Oct	62	45
Nov	13	13	Dec	5	2

where t = time, I = count interval in minutes and F = the number of feeding birds. The number of birds feeding in each count was compared with the maximum number feeding over the low tide period rather than the total number of birds present in that count. This was in order to avoid inclusion of the occasional transient groups of (usually) nonfeeding Whimbrels. Apart from these visitors, observations of colour-ringed and distinctively marked Whimbrels indicated their tendency for site-faithfulness. Grey Plovers held fixed territories on the study area, so that *Fmax* usually equalled the total number of birds present.

Foraging Whimbrels were selected randomly for focal observations. By day, they were aged according to body fatness and plumage characteristics. Juveniles at this time of year are very much leaner than adults and are in worn plumage whereas adults are in fresh plumage. Birds were aged at night on body condition alone. Some individuals, probably second year birds, could not be positively identified as fully adult in the field, and were excluded from all analyses. During each observation, the number of steps and pecks were counted, all prey items recorded and aggressive interactions were timed. The method of prey capture was recorded as visual or tactile. Not all probes were considered as tactile foraging, as there were several visual cues that Whimbrels could use prior to probing, including the size of the burrow entrance, and water movement caused by prawns irrigating their burrows (Martin 1991). Foraging was thus only recorded as tactile when prey were captured during multiple "stitching" probes.

On the basis of previous observations, all Grey Plovers could be identified individually using a combination of plumage characteristics and territory boundaries or from colour-rings, and five adult birds were chosen for detailed study. Due to their small number, the focal birds could not be randomly selected. The observation periods were thus of approximately 15 min duration, with data recorded separately for each minute, but were stopped if a bird began roosting. These 1-min focal observations were considered as independent samples for statistical analysis, for the following reasons: observations commenced randomly within the foraging bout and, because prawns surfaced throughout the tidal period (Martin 1991), the capture of prey during

one minute did not affect the probability of prey capture in subsequent minutes, as would have been the case in a situation of prey depletion. Because of the move-stop-search foraging method of Grey Plovers (described in detail by Pienkowski 1983), the number of steps in each move was counted and the outcome of each move was recorded as a failed attack, prey capture or search pause. Aggressive interactions and periods spent searching for prey were timed.

The methods for calculating energy intake rates are described in Chapter 1. In order to calibrate prey size estimates, prawns were held in the bills of a stuffed Grey Plover and Whimbrel, and their size was estimated using the same equipment and from the same distance as in the field. Figure 3.1 shows the regressions of estimated to actual prawn lengths that were used to calibrate field estimates. It was not possible to perform this experiment at night for Grey Plovers, so we used the daytime regression line in all Grey Plover calculations. Prey other than prawns and crabs are eaten by both species. Although crabs with a carapace width of <5mm could be recognized in the field, other prey items were so small that they could not be identified. Martin (1991) concluded that the energy contribution of these prey, which in his study comprised 33 - 36% of the numerical intake of Grey Plovers and Whimbrels at the Zwartkops estuary, was between 0.4% and 0.8%. In this study, small unidentified prey accounted for even less of the numerical intake (18% and 13% for Grey Plovers and Whimbrels respectively). Thus the energetic contribution of these prey was probably very small and they were excluded from calculations of energy intake rate but were included in calculations of prey capture rate.

Three allometric equations relating body mass to energy intake rate (EIR) and daily energy expenditure (DEE) were used for comparison with the field observations:

EIR (kJ/min) = $2.02W(g)^{0.68}$ (all guilds except seabirds, from field observations of EIR, Bryant & Westerterp 1980);

DEE = $10.9W(g)^{0.640}$ (all guilds, using doubly-labelled water in free-living birds, Nagy 1987); and

DEE = $0.912W(kg)^{0.704}$ (waders, from net energy consumption by caged birds at 10°C, Kersten & Piersma 1987),

where W is the wet mass. The mean weights used were those of birds caught by mist-netting on the Zwartkops estuary during the study period. The calculations of EIR, above, were converted to net energy intake using an assimilation efficiency value of 70%. In addition, estimates of the daily energy requirements of adult birds, based on lean body mass and the energy required to lay down premigratory reserves (Chapter 1) was used for comparison.

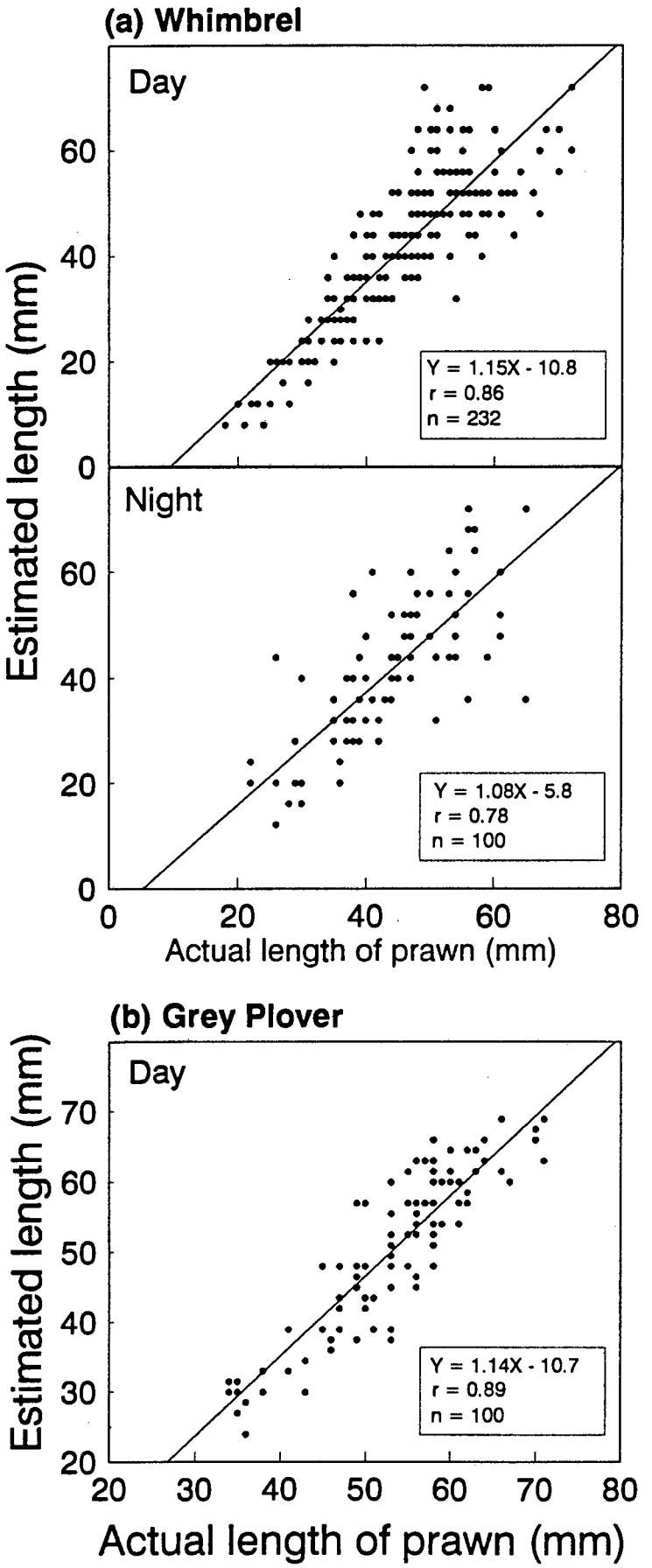


Figure 3.1. Estimated vs actual length of *Upogebia* prawns held in the bill of a stuffed Whimbrel during the day and at night, and Grey Plover during the day, and the equations used to calibrate observer estimates.

RESULTS

Foraging activity and behaviour

The number of birds foraging by day and night at comparable tidal levels did not differ for either species (Wilcoxon test, Grey Plovers $T = 18.5$, $P > 0.1$; Whimbrels $T = 22$, $P > 0.1$; Fig. 3.2).

Grey Plovers foraged exclusively visually and, qualitatively, their foraging behaviour was the same by day and night and did not differ between moonlit and moonless nights.

Whimbrels were predominantly visual foragers by day and night, but they also fed tactilely for some of the time. The proportion of prawns caught tactilely during the day (2/52) and at night (3/47) did not differ significantly ($X^2_1 = 0.31$, $P > 0.05$). During the day, Whimbrels foraged very differently to Grey Plovers, moving continuously across the mudflat and pecking or probing *en route*. At night, their foraging behaviour was intermediate between their daytime behaviour and that of Grey Plovers. Although they did forage by continuous walking, they also stopped regularly to search for prey at night.

Grey Plovers defended the same territories at night as during the day. Territorial encounters involved posturing and parallel walking, and ranged in duration from 16 to 360 seconds (mean 120 $\pm$ 92 (S.D.) s, $n = 20$). The overall proportion of foraging time spent in territorial defence by day and night was very similar (6.7% *vs* 6.5%). Whimbrels, feeding on the same mudflat and on the same prey as Grey Plovers, were not territorial. Aggressive interactions were largely restricted to short ground chases averaging 6.9 $\pm$ 11.1 (S.D.) s ($n = 46$). Whimbrels spent far less cumulative time in aggressive encounters than did Grey Plovers. During the day they were widely dispersed across the mudflat and only 0.8% of their foraging time was spent in aggression. At night, Whimbrels were more clumped, foraging close to the water's edge, and aggression accounted for 1.8% of their foraging time.

Foraging effort and success

Grey Plovers took significantly fewer steps, and made fewer moves and attacks per minute at night than during the day (Table 3.2). The average duration of searches was significantly longer at night than during the day (4.1 $\pm$ 3.2 (S.D.) *vs* 3.0 $\pm$ 2.9 (S.D.) s, $n = 313, 296$, *t*-test, $t = 4.7$, $P < 0.001$). In addition to making fewer moves at night, a greater proportion of moves comprised a low number of steps ($X^2_8 = 47.94$, $P < 0.001$; Fig. 3.3a), resulting in an overall reduction in the distance covered at night. During the day, Grey Plovers took significantly more steps to catch prey than at night (Mann-Whitney *U*-test, $U = -2.98$, $P < 0.01$; Fig. 3.4), suggesting that they were

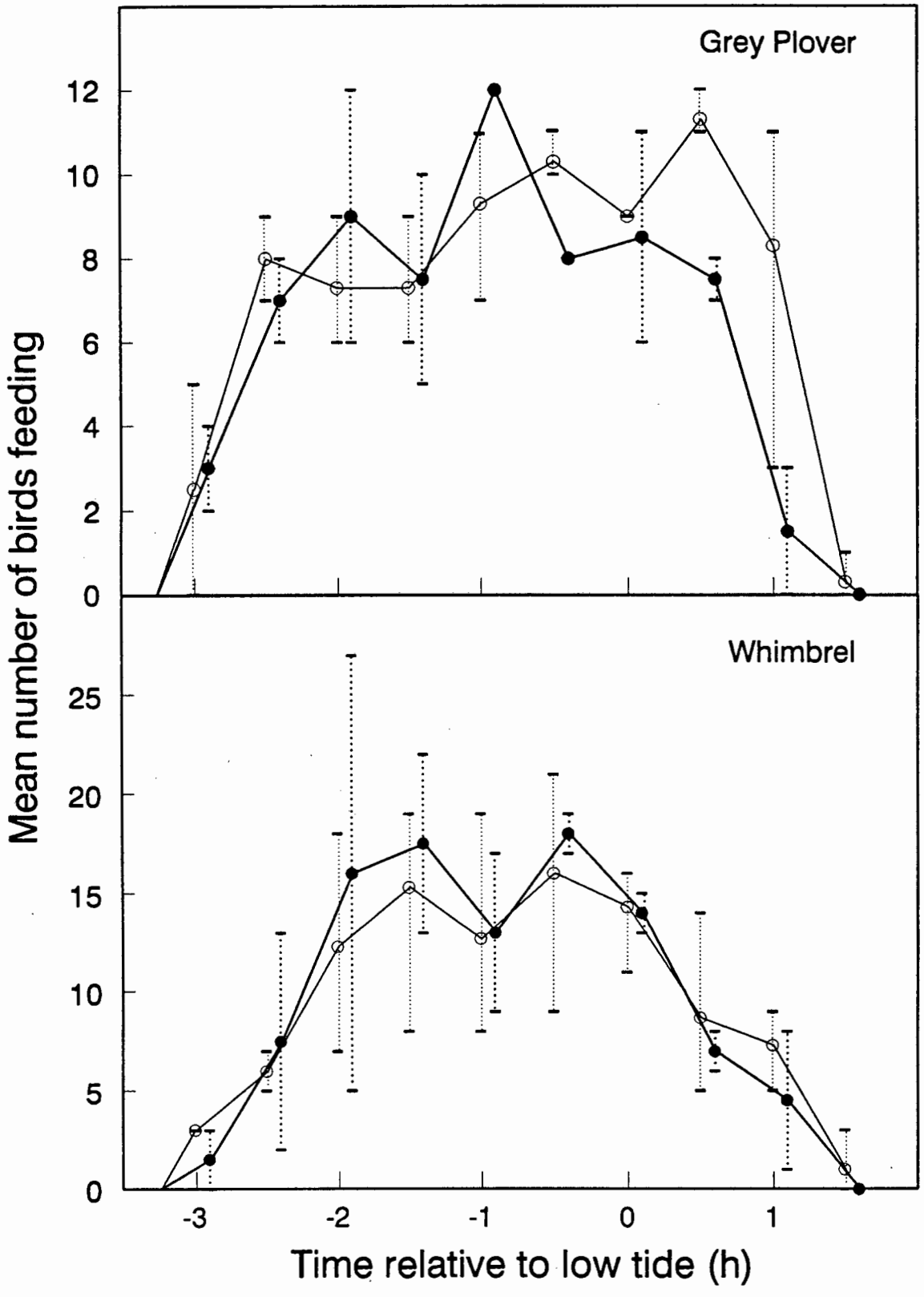


Figure 3.2. Mean number (± range) of Grey Plovers and Whimbrels foraging on the Zwartkops study area by day (open circles) and night (solid circles) relative to the time of low tide.

Table 3.2. Average (± S.D.) number of steps, moves and attacks, and average number of prey and net energy intake (kJ) obtained per minute by Grey Plovers feeding by day and by night, and on moonlit *vs* moonless nights.

	Steps	Moves	Attacks		Prey captured (*n*)			Net energy intake (kJ)
			n	% success	Crabs	Prawns	Total#	
Day	63.9	8.3	1.3	51	0.37	0.16	0.66	1.19
(*n* = 309)	(40.6)	(4.5)						
	**	**	*		*	*n.s.*	**	*n.s.*
Night	53.2	7.4	0.9	27	0.05	0.15	0.25	1.15
(*n* = 299)	(38.7)	(3.5)						
Moonlit	52.8	7.6	1.17	22	0.06	0.16	0.26	1.27
(*n* = 145)	(41.0)	(3.6)						
	n.s.	*n.s.*	*		*n.s.*	*n.s.*	*n.s.*	*n.s.*
Moonless	53.6	7.2	0.69	35	0.04	0.14	0.24	1.04
(*n* = 154)	(36.7)	(3.4)						

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Steps and moves: Student's *t*-test; all others: Sampled Randomization Test

Includes unidentified prey items

able to locate prey from a greater distance. The proportion of attacks which were successful by day was almost double that at night (Table 3.2). Although crabs were captured at a significantly faster rate during the day, the rate of prawn capture did not differ between day and night (Table 3.2), nor did the sizes of prawns taken (total length 52 ± 13 (S.D.) mm *vs* 55 ± 12 (S.D.) mm, *t*-test, $t = -1.34$, $P = 0.18$; Fig. 3.5a). The net energy intake rate of Grey Plovers was marginally, but not significantly, lower at night than during the day (Table 3.2).

On a moonless night, the attack rate of Grey Plovers was significantly lower than on a moonlit night, but there were no differences in the frequency of prey capture, foraging effort (steps and moves) or energy intake rate (Table 3.2).

There was some variability in the way that individual Grey Plovers changed their foraging behaviour from day to night (Table 3.3). Of the five individuals studied, two apparently foraged most efficiently by night whereas the other three were most efficient by day, but this difference was only significant for one bird. Much longer observation periods are required to make firm conclusions about individual differences.

Both adult and juvenile Whimbrels took significantly more steps per minute by day than at night, but there were no differences in the frequency with which they attacked prey (Table 3.4). Significantly fewer steps were taken between capture attempts at night ($X^2_5 = 34.95$, $P < 0.001$; Fig. 3.3b). Only adults were seen to eat crabs: they captured crabs less frequently at night than by day, but the difference was not significant (Table 3.4). There was no signficant difference in the frequency with which adults or juveniles captured prawns by day and night (Table 3.4), nor between

Table 3.3. Average (± S.D.) number of steps, moves, attacks and net energy intake (kJ) per minute by day and by night of five individual Grey Plovers (A-E), based on two hours' observation per bird.

	Steps		Moves		Attacks *n*		Attacks % success		Net energy intake (kJ)	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
A	67 *n.s.* 61 (51.2) (25.4)		6.4 *n.s.* 7.8 (4.4) (2.8)		0.44 *n.s.* 0.61		41	36	0.69 *n.s.* 2.17	
B	66 *** 39 (42.8) (43.5)		8.2 ** 6.5 (3.9) (3.3)		1.03 *n.s.* 1.10		34	16	0.92 *n.s.* 1.49	
C	71 *n.s.* 70 (42.7) (40.8)		8.5 *n.s.* 8.8 (4.1) (3.8)		0.86 *n.s.* 0.70		61	33	1.69 *n.s.* 1.08	
D	59 *n.s.* 58 (32.5) (40.6)		8.9 *n.s.* 7.6 (5.1) (3.7)		2.12 * 1.27		38	26	1.48 * 0.58	
E	56 ** 40 (29.7) (28.5)		9.4 *** 6.4 (4.4) (3.2)		1.95 ** 0.93		72	29	1.24 *n.s.* 0.54	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Steps and moves: Student's t-test; all others: Sampled Randomization Test

Table 3.4. Average (± S.D.) number of steps and pecks, and average number of prey and net energy intake (kJ) obtained per minute by Whimbrels feeding by day and by night.

	Steps	Pecks	Prey captured (*n*) Crabs	Prawns	Total#	Net energy intake (kJ)
Adults						
Day (*n* = 156)	95 (40)	5.9 (4.4)	0.21	0.27	0.56	1.53
	***	*n.s.*	*n.s.*	*n.s.*	***	*n.s.*
Night (*n* = 141)	57 (33)	6.8 (5.3)	0.11	0.20	0.31	1.24
Juveniles						
Day (*n* = 29)	117 (45)	9.6 (5.0)	0	0.14	0.24	1.10
	***	*n.s.*		*n.s.*	*n.s.*	*n.s.*
Night (*n* = 22)	68 (29)	7.5 (4.5)	0	0.14	0.14	0.97
Adults *vs* juveniles						
Day	**	***	*n.s.*	*n.s.*	*n.s.*	*n.s.*
Night	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Steps and pecks: Student's t-test; all others: Sampled Randomization Test.

Includes unidentified prey items

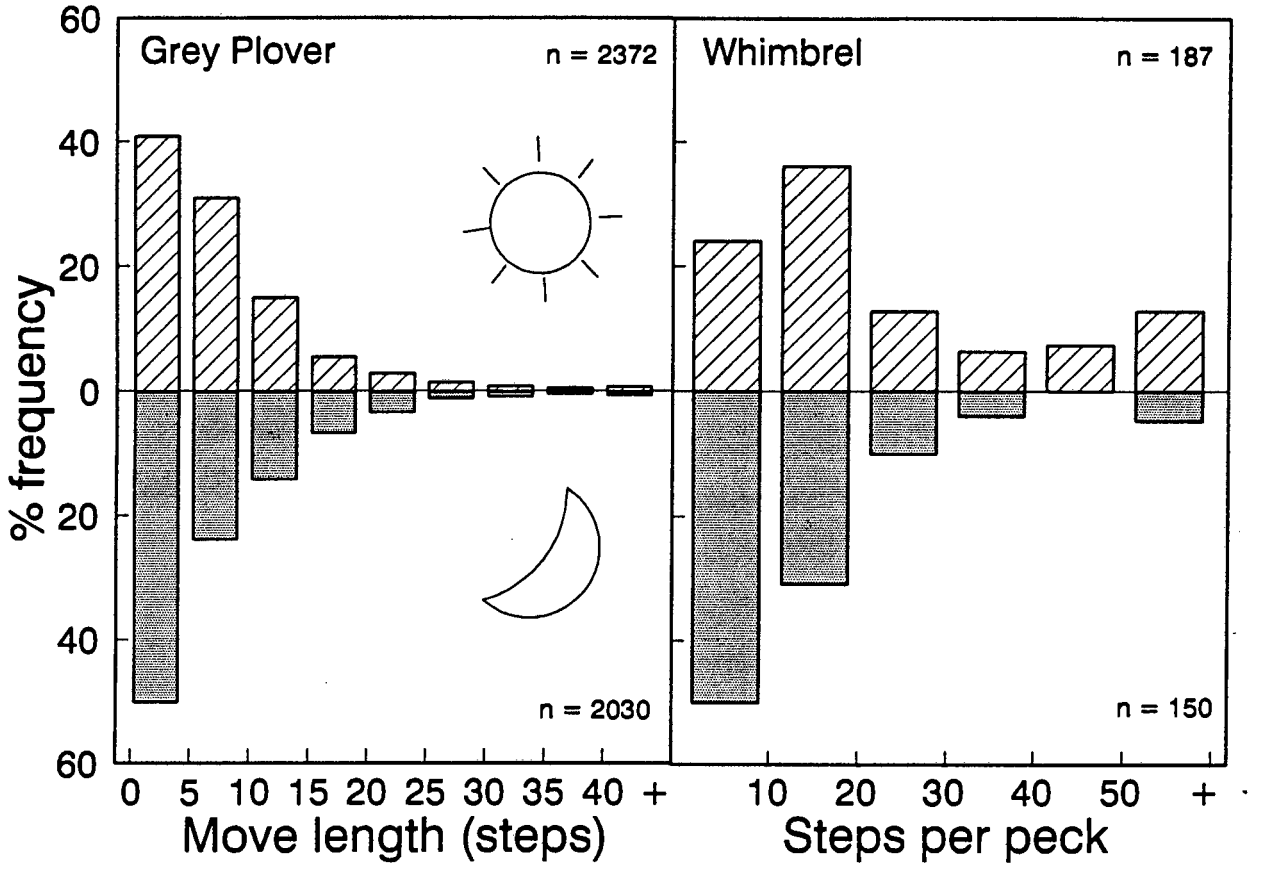


Figure 3.3. Number of steps taken per foraging move by Grey Plovers and the number of steps taken between pecks by Whimbrels by day (hatched bars) and night (solid bars).

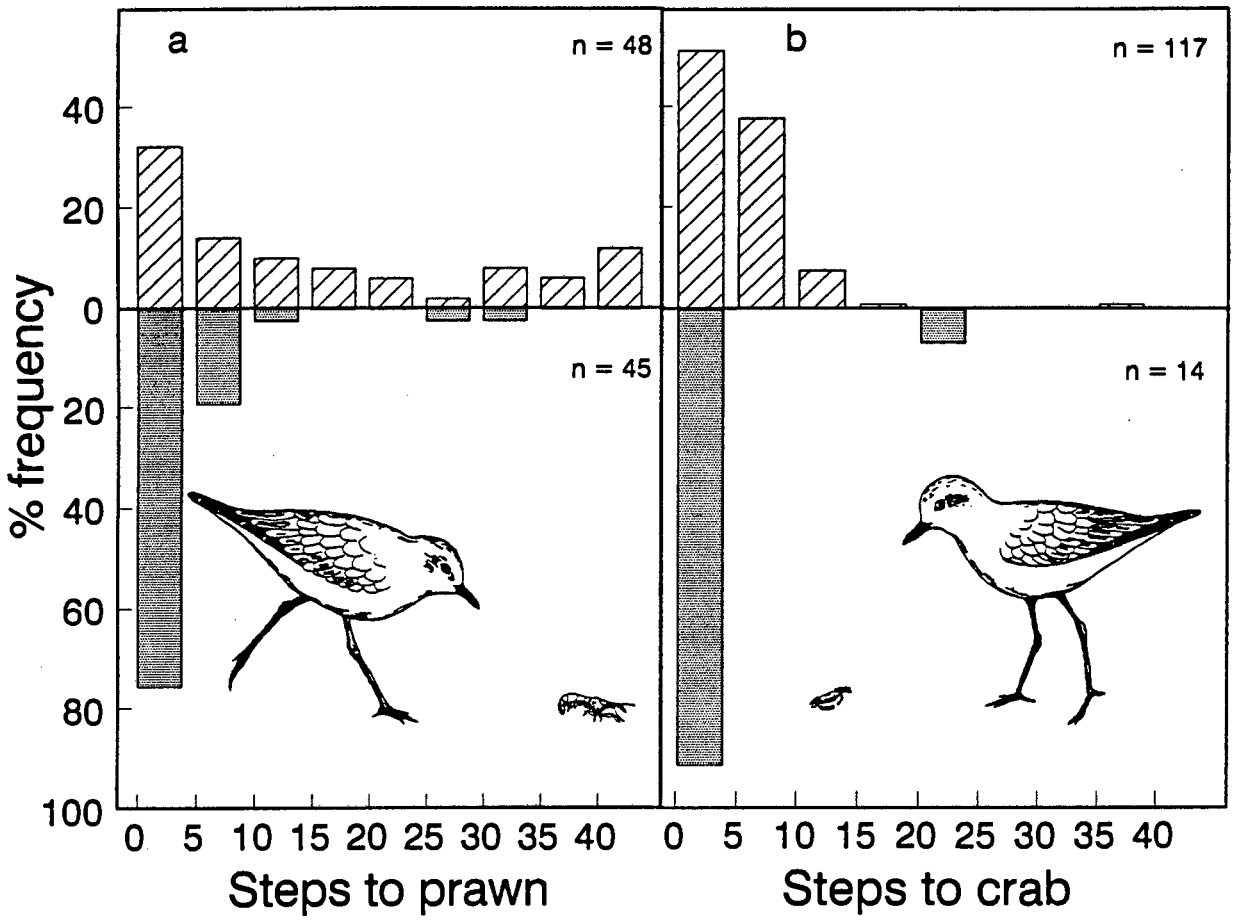


Figure 3.4. Number of steps taken per move by Grey Plovers to catch (a) prawns and (b) crabs by day (hatched bars) and night (solid bars).

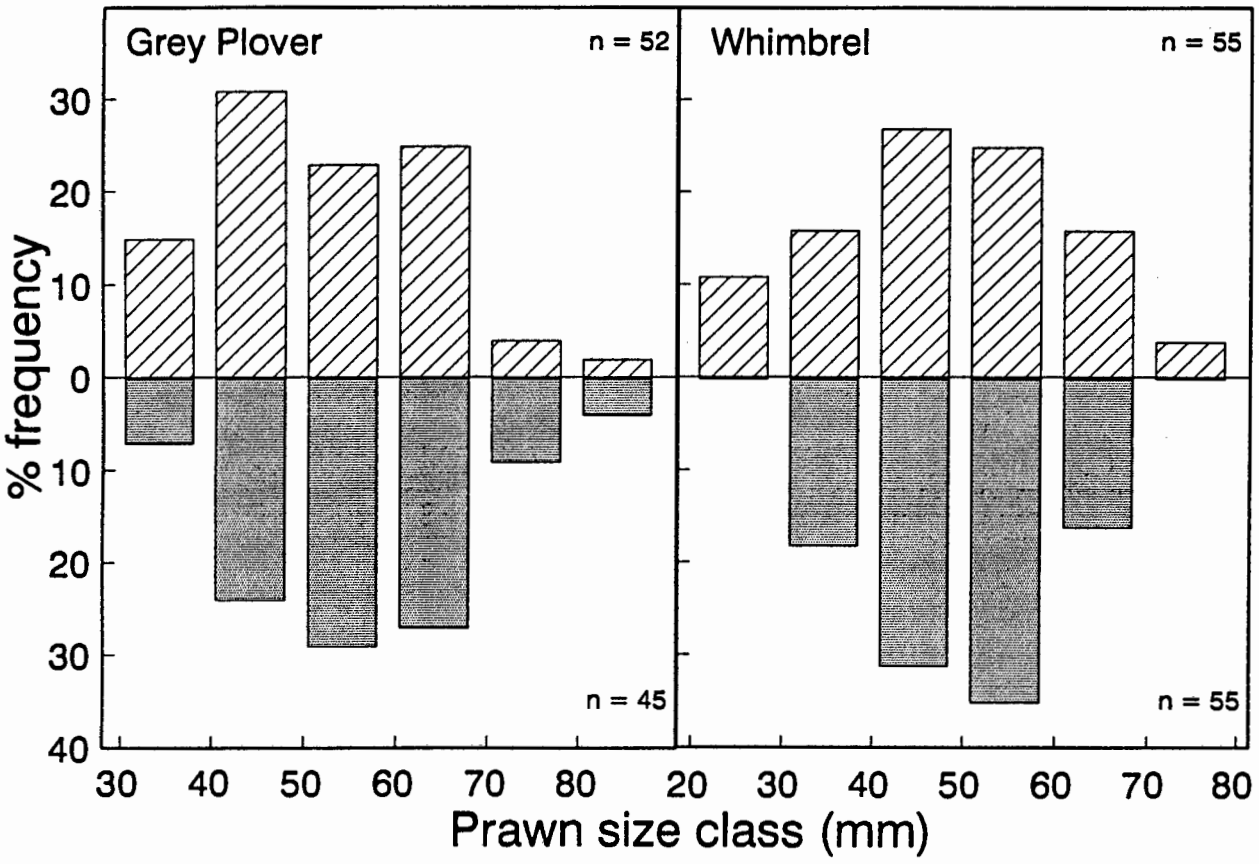


Figure 3.5. Size distribution of *Upogebia* prawns eaten by Grey Plovers and Whimbrels by day (hatched bars) and night (solid bars).

Table 3.5. Total day and night low-tide foraging time, net energy intake rate and total net energy gain by Grey Plovers and Whimbrels. These are compared with allometric predictions of energy intake rate (Bryant & Westerterp 1980) and daily energy requirements (a: Nagy 1987, b: Kersten & Piersma 1987, c: Chapter 1).

		Foraging time (min)	Energy intake rate (kJ/min)		Total energy intake (kJ)			
			observed	predicted	observed	predicted *a*	predicted *b*	predicted *c*
Grey Plover	Day	195	1.19	0.96	232			
	Night	160	1.15		184			
	TOTAL				416	358	328	401
Whimbrel Adult	Day	181	1.53	1.77	277			
	Night	165	1.24		205			
	TOTAL				482	635	616	646
Juvenile	Day	181	1.10	1.34	199			
	Night	165	0.97		160			
	TOTAL				359	482	455	

the sizes of prawns taken (by both age classes combined, 49 ± 13 (S.D.) mm *vs* 50 ± 9 (S.D.) mm, *t*-test, $t = -0.67$, $P = 0.50$; Fig. 3.5b). Energy intake rates did not differ significantly between day and night for adult or juvenile Whimbrels. Juveniles took more steps per unit time and pecked more frequently than adults during the day, but there were no significant differences between the age classes in energy intake rates either during the day or at night (Table 3.4).

Nocturnal contribution to daily energy intake

The combination of slightly (though not significantly) lowered foraging efficiency at night, and reduced foraging time, resulted in the total night-time energy intake of both Grey Plovers and Whimbrels being slightly lower than during the day (Table 3.5). Grey Plovers, adult and juvenile Whimbrels achieved, respectively, 44%, 43% and 45% of their daily low-tide period energy intake at night.

DISCUSSION

Foraging activity and behaviour

It has been well established that obligate visual foragers, such as Grey Plovers, continue to forage visually at night (Pienkowski 1981, 1982), and it has been suggested that the large eyes of such species are an adaptation to night activity (Dugan 1981, Pienkowski 1983). Species such as Whimbrels, which commonly use both visual and tactile foraging methods, are expected to forage predominantly tactilely at night: this has been demonstrated for several species, including Eurasian Oystercatchers *Haematopus ostralegus*, *Tringa* species and Blackwinged Stilts *Himantopus himantopus* (Hulscher 1976, Sutherland 1982b, Robert & McNeil 1989). However, Whimbrels fed predominantly visually both by day and night at the Zwartkops estuary. This was probably due to the relatively large size and the behaviour of the prawns.

Both Grey Plovers and Whimbrels changed their foraging behaviour in response to reduced visibility at night. Grey Plovers made fewer, shorter foraging movements at night, and these were interspersed with longer periods of searching. The shorter moves between searches indicate a reduction in search radius. This was compensated for by increasing the search time rather than increasing the number of moves, or distance travelled. Further evidence for a real reduction in visual acuity at night were the shorter distances moved to attack prey (Fig. 3.4). The frequency of pecks by Grey Plovers decreased at night in proportion to the number of steps taken, and more prey capture attempts were made on moonlit than on moonless nights. Whimbrels moved more slowly when foraging at night and, unlike during the day, frequently stopped to search. However, there was no corresponding reduction in their peck rate. The higher proportion of failed prey capture attempts in both species at night suggests that they were less able to identify prey successfully, but the reduction in number of attacks made by Grey Plovers at night implies that they were better at identifying potential prey than Whimbrels.

Despite the fact that both species searched a smaller area per unit time at night, the rate of prawn capture by day and night did not differ for either species. This suggests that an individual bird at night caught a higher proportion of the prawns it saw. Capture rates may also have been enhanced by the use of olfactory cues in prey detection. The probability of more than one bird seeing, and thus competing for, the same prawn was probably reduced at night, i.e. the intensity of exploitative competition was lower. Interference competition, on the other hand, appeared to be as intense at night as during the day. Grey Plovers retained their daytime territories at night and defended them with the same intensity as during the day. Grey Plovers at Teesmouth, northeast England, also retain the same territories by day and night (Dugan 1981,

Pienkowski 1983, Wood 1986).

Whimbrels fed closer together at night than by day, possibly as a result of their reduced search range. During the day, when Whimbrels frequently locate prey from a considerable distance, it is presumably advantageous for them to spread out to avoid interference competition from neighbours. At night, when visibility is reduced, birds are able to concentrate in the most productive feeding areas.

Whimbrels and Grey Plovers caught fewer crabs at night than during the day, although the difference was not significant for Whimbrels. Whilst the relative availability of crabs at night is not known, this may simply reflect an inability of the birds to locate crabs due to their small size and crypsis, rather than a change in availability or deliberate avoidance. Furthermore, Grey Plovers and Whimbrels caught fewer of the smaller size classes of prawns at night (Fig. 3.5).

Despite the changes in step and peck rates and in prey capture rates of Grey Plovers and Whimbrels foraging at night, there were no significant differences in their rates of energy intake. It can be concluded, therefore, that extrapolations based on variation in such indirect measures of energy intake rate will frequently be wrong.

The importance of nocturnal foraging

Grey Plovers and Whimbrels at the Zwartkops estuary had similar rates of energy intake by day and by night, whereas Whimbrels feeding on crabs in North Africa only achieved 17 - 58% of their daytime intake rates at night (Zwarts & Dirksen 1990). This highlights the importance of prey type and behaviour in the contribution that nocturnal foraging can make to daily energy intake.

Several factors may promote night-time foraging, including increased prey availability at night (Dugan 1981, Pienkowski 1983, Robert & McNeil 1989), avoidance of predators (Robert, McNeil & Leduc 1989) or simply failure to satisfy their energy demands during the day (e.g. Goss-Custard 1969, Heppleston 1971). At the Zwartkops estuary there is no increase in prey availability at night and avian predation is uncommon. However, neither Grey Plovers nor Whimbrels were able to satisfy their predicted energy demands during the daytime low tide period (Table 3.5).

Grey Plover energy intake rates and total intake exceeded allometric predictions by at least 16% (Bryant & Westerterp 1980, Nagy 1987, Kersten & Piersma 1987; Table 3.5). The third prediction of daily energy requirements took into account the additional energy needed to increase mass prior to migration (Chapter 1), and total daily intake of Grey Plovers was close to this amount (Table 3.5). The energy intake rates and total intake of adult and juvenile Whimbrels, however, fell below all the predictions by 21% - 26% (Table 3.5). Whereas the territorial Grey Plovers were never observed to feed elsewhere when the mudflats were inundated, Whimbrels

usually fed on crabs in the saltmarshes at high tide. Whimbrels could not be observed during these periods, and thus their total daily intake could not be calculated. Nevertheless, by 14 March, 11 adult Whimbrels at the Zwartkops estuary had increased their mass by an average of 37% (with respect to lean mass calculated from wing lengths (Zwarts *et al.* 1990c)), which suggests that Whimbrels were making up the apparent energy deficit between low tide periods.

Several observational studies of waders have indicated negative energy budgets, relative to allometric predictions, both during the breeding season (Semipalmated Sandpiper *Calidris pusilla*: Ashkenzie & Safriel 1979) and during the non-breeding season (Grey Plovers: Schramm 1978, Dugan 1981, Pienkowski 1982, Martin 1991; Curlew Sandpipers *Calidris ferruginea*: Puttick 1980). Dugan (1981) reported that the deficit in the daily energy intake of Grey Plovers in northwestern Europe ranges between 37% and 93% of predicted requirements. These observations suggest either that the predictions made by allometric equations are too high or that observers have been unable to quantify rates of energy gain accurately. This study demonstrates that Grey Plovers at the Zwartkops estuary were able to meet their daily energy requirements during the pre-migration period, and it is probable that Whimbrels were able to balance the low-tide energy deficit by foraging elsewhere during the high tide period.

The apparent energy deficits reported for waders in several studies are probably in part a consequence of problems in quantifying energy intake rates due to the nature of the prey base and problems in determining nocturnal intake rates. The findings in this study caution against making inferences about nocturnal energy intake rate based solely on extrapolation from parameters of foraging behaviour such as attack frequency.

Appendix 3.1. Intertidally-foraging waders which have been recorded as feeding at night in north temperate (NT), tropical (T) and south temperate (ST) latitudes. Where nocturnal foraging is recorded in more than one region, references for the different regions are separated with a semi-colon.

Species	NT	T	ST	References
DROMADIDAE				
Crab Plover *Dromas ardeola*		X		Cramp & Simmons 1983
HAEMATOPODIDAE				
Eurasian Oystercatcher *Haematopus ostralegus*	X	X		Drinnan 1957, 1958a,b, Davidson 1968, Heppleston 1971, Dare & Mercer 1973, Hulscher 1974, 1976, 1982, Greenhalgh 1975, Zwarts & Drent 1981, Swennen 1990, Sutherland 1982a,b; Zwarts et al. 1990b
American Pied Oystercatcher *H. palliatus*		X		Burger 1984
African Black Oystercatcher *H. moquini*			X	Hockey 1984, Hockey & Underhill 1984, Martin 1991
RECURVIROSTRIDAE				
Blacknecked Stilt *Himantopus mexicanus*		X		McNeil & Robert 1988
Blackwinged stilt *H. himantopus*			X	This study
Avocet *Recurvirostra avosetta*			X	C.R. Velasquez, L. Vanherck pers. comm.
CHARADRIIDAE				
Northern Lapwing *Vanellus vanellus*	X			Spencer 1953, Hale 1980
Blacksmith Plover *V. armatus*			X	B. Kalejta, pers. comm.
Eurasian Golden Plover *Pluvialis apricaria*	X			Hale 1980
Grey Plover *P. squatarola*	X	X	X	Evans 1976, Dugan 1981, Pienkowski 1983, Wood 1986; Zwarts et al. 1990b; Schramm 1978, Martin 1991, this study
Ringed Plover *Charadrius hiaticula*	X	X	X	Pienkowski 1983; Zwarts et al. 1990b; B. Kalejta, pers. comm.
Wilson's Plover *C. wilsonia*		X		Morrier & McNeil 1991.

Appendix 3.1 continued

Species	NT	T	ST	References
Piping Plover *C. melodus*	X			Burger 1984
Kittlitz's Plover *C. pecuarius*			X	B. Kalejta, C. Velasquez, pers. comm.
Kentish Plover *C. alexandrinus*		X		Zwarts et al. 1990b
Whitefronted Plover *C. marginatus*			X	This study
Doublebanded Plover *C. bicinctus*			X	Lane 1987
Greater Sandplover *C. leschenaultii*		X	X	This study
Shore Plover *Thinornis novaeseelandiae*			X	Phillips 1977
SCOLOPACIDAE				
Bartailed Godwit *Limosa lapponica*	X	X	X	Smith & Evans 1973, Evans 1976; Zwarts et al. 1990b; this study
Whimbrel *Numenius phaeopus*		X	X	Zwarts et al. 1990b; Martin 1991, this study
Eurasian Curlew *N. arquata*	X	X	X	Evans 1976, Hale 1980; Zwarts et al. 1990b; Martin 1991
Far Eastern Curlew *N. madagascariensis*			X	Dann 1986
Redshank *Tringa totanus*	X	X		Goss-Custard 1969, 1970, Evans 1976, Baker 1981, Zwarts et al. 1990b
Greenshank *T. nebularia*		X	X	Zwarts *et al.* 1990b, this study; Tree 1978, Martin 1991
Greater Yellowlegs *Tringa melanoleuca*		X		McNeil & Robert 1988
Lesser Yellowlegs *Tringa flavipes*		X		McNeil & Robert 1988
Willet *Catoptrophorus semipalmatus*	X	X		Stenzel *et al.* 1976, Burger 1984; Robert *et al.* 1989
Terek Sandpiper *Xenus cinereus*		X	X	This study

Appendix 3.1 continued

Species	NT	T	ST	References
Spotted Sandpiper *Actitis macularia*		X		Gochfeld 1971
Ruddy Turnstone *Arenaria interpres*	X	X	X	Burger 1984; Alterogt & Davis 1980, this study; Martin 1991
Shortbilled Dowitcher *Limnodromus griseus*	X	X		Bent 1962; Robert *et al.* 1989
Red Knot *Calidris canutus*	X	X		Prater 1972; Zwarts et al. 1990b
Sanderling *C. alba*	X		X	Greenhalgh 1975, Burger 1984; this study
Semipalmated Sandpiper *C. pusilla*		X		Robert *et al.* 1989
Western Sandpiper *C. mauri*		X		Robert *et al.* 1989
Little Stint *C. minuta*		X	X	Zwarts et al. 1990b; B. Kaljeta, pers. comm.
Least Sandpiper *C. minutilla*		X		Robert *et al.* 1989
Sharptailed Sandpiper *Calidris acuminata*			X	Dann 1981
Dunlin *C. alpina*	X	X		Mascher 1966, Evans 1976, Zwarts *et al.* 1990b, Mouritsen 1992
Curlew Sandpiper *C. ferruginea*		X	X	Zwarts *et al.* 1990b; this study

Sites included in this study are: south temperate - Marcus Island, SW Cape, South Africa (33°03S, 17°58E) and the Zwartkops estuary, E. Cape, South Africa (33°52'S, 25°38'E); tropical - Mauritius, Indian Ocean (20°15'S, 57°35'E). Personal communications from C. Velasquez and B. Kalejta are observations made at the Berg River estuary, W. Cape, South Africa (32°47'S, 18°10'E).

Appendix 3.2. Ratios of nocturnal/diurnal pecking or probing rates (PR), numerical prey intake rates (NIR) and energy intake rates (EIR) for waders which forage intertidally.

Species	Data type	Time*	Night/day ratio PR	NIR	EIR	Site	Comments	References
Eurasian Oystercatcher	FO	1		0.85		W. Europe	Edible cockles *Cerastoderma edule*	Davidson 1968
	FO	2		1.00		W. Europe	Calculated from number of cockle shells left opened on mudflat	Drinnan 1957
	CA	2			0.47-0.60	W. Europe	Food *ad lib.*	Drinnan 1958a
	CA	?			0.58	W. Europe	Single bird fed *ad lib.*	Heppleston 1971
	CA	2			0.86	W. Europe	Non-tidal schedule	Hulscher 1974
	CA	2			1.45	W. Europe	Tidal schedule	Hulscher 1974
	FO	2			0.10	W. Europe	Gut contents, moonless nights	Greenhalgh 1975
	CF	2			1.00	W. Europe	Bivalves and crabs	Hulscher 1976
	FO	1		0.48	0.36	W. Europe	Edible cockles *Cerastoderma edule*	Sutherland 1982a,b
	FO	1		0.98		W. Europe	Giant bloody cockles *Anadara senilis*	Swennen 1990
African Black Oystercatcher	FO	2		0.36		S. Africa	Chick shell-middens	Hockey & Underhill 1984
Grey Plover	FO	1	0.51, 0.97			W. Europe	Moonless, moonlit nights; polychaetes *Notomastis latericeus* and *Arenicola marina*	Pienkowski 1983
	FO	1	0.62			W. Europe	Polychaetes *Nereis diversicolor*	Evans 1976
	FO	1	0.92, 0.84	0.82, 0.38		S. Africa	Moonlit, moonless; mudprawn *Upogebia africana* only, small prey ignored	Martin 1991
	FO	1 2	0.71	0.38	0.93 0.76	S. Africa	Mudprawn *U. africana*, and small crabs *Cleistostoma* spp.	This study
Ringed Plover	FO	1	0.41, 0.85			W. Europe	Moonless - June, July; amphipod *Bathyporeia pelagica* and isopod *Eurydice pulchra*	Pienkowski 1983
Bartailed Godwit	FO	1	0.96, 0.62			W. Europe	Peck, probe; polychaete *N. diversicolor*	Greenhalgh 1975
Whimbrel	FO	1			0.17, 0.24, 0.58	Mauritania	Single bird; Feb, Mar, Apr; Fiddler crab *Uca tangeri*	Zwarts & Dirksen 1990
	FO	1	1.05 0.37			S. Africa	Moonlit nights, mudprawn *U. africana* only, small prey ignored	Martin 1991
	FO	1 (a) (j) 2 (a) (j)	1.17 0.78	0.55 0.58	1.05 1.04 0.96 0.76	S. Africa	Mudprawn *U. africana* (adults and juveniles) and small crabs *Cleistostoma* spp. (adults only).	This study*

Appendix 3.2 continued.

Species	Data type	Time*	Night/day ratio PR	NIR	EIR	Site	Comments	References
Redshank	FO	2		0.76, 0.06		W. Europe	Stomach contents; moonless, moonlit; gastropod *Hydrobia ulvae* and amphipod *Corophium volutator*	Greenhalgh 1975
Greenshank	FO	1	1.08, 0.87	1.00, 0.69		S. Africa	Moonlit, moonless; mudprawn *U. africana* only.	Martin 1991
Ruddy Turnstone	FO	1	1.11	0#		S. Africa	Mudprawn *U. africana*; based on 24 minutes night obs. #Turnstones at this site do eat *U. africana* at night - pers. obs.	Martin 1991
Red Knot	FO	2		0.24		W. Europe	Bivalve *Macoma balthica* only; gizzard contents	Prater 1972
	FO	1	0.14			W. Europe	Bivalve *M. balthica*; moonlit, moonless nights	Greenhalgh 1975
		2		0.24			Gastropod *H. ulvae* only, gizzards	
	FO	1	0.53			W. Europe	Gastropod *H. ulvae* and amphipod *C. volutator*, moonlit nights	Greenhalgh 1975
Sanderling	FO	1	0.65			W. Europe	Moonlit nights, mainly amphipod *Bathyporeia pelagica*	Greenhalgh 1975
Curlew Sandpiper	FO	1	1.34	0		S. Africa	14 minutes of night observation; mudprawn *U. africana* only	Martin 1991

* 1 = recorded per unit active foraging time, 2 = includes non-foraging periods, e.g. recorded over a complete tidal cycle.

SECTION II

CHAPTER 4

VARIATION IN THE DIET AND FORAGING BEHAVIOUR OF GREY PLOVERS AND WHIMBRELS IN TROPICAL AND SOUTH TEMPERATE WETLANDS

SUMMARY

1. Between-site variation in the diet and foraging behaviour of a fixed-method forager, the Grey Plover, and a versatile forager, the Whimbrel, was examined and compared.

2. Both species ate a variety of prey species depending on their availability. Grey Plover diets were dominated by polychaetes and crabs, and Whimbrels ate mostly crabs; both species consumed large surface-active mudprawns when available. Of the two, Whimbrels were the more specialised in prey choice.

3. Grey Plovers always forage in a run-stop-search manner, but changed the emphasis of components of this behaviour in response to prey type. Whimbrels foraged tactilely or visually, depending on prey visibility, both in water and on mud, and readily changed foraging speed and habitat.

4. Grey Plover densities appeared to have an upper limit, probably because of the space required for their stereotyped foraging behaviour. Whimbrel densities were highly variable, and were affected by prey type and foraging methods. Foraging time was a fairly constant proportion of tidal exposure time at most sites, and nocturnal foraging was observed at all sites visited at night. Daytime energy intake rates of both species varied between sites, and reasons for this variability were discussed. Evidence suggested that birds foraged maximally at all sites in order to meet their daily energy requirements.

5. The stereotyped visual, run-stop-search foraging method of plovers is probably related to a limited ability to focus whilst moving as well as to their having relatively insensitive, short bills. The broader diversity of prey types consumed by Grey Plovers was attributed to limitations imposed by obligate visual foraging, whereas the flexible foraging behaviour of Whimbrels allowed the latter to concentrate their efforts on the most profitable prey.

6. The limits to the nonbreeding distributions of Grey Plovers and Whimbrels are influenced by a combination of body size and behavioural and morphological foraging limitations.

INTRODUCTION

Many shorebird species migrate long distances to spend the nonbreeding season in coastal wetland habitats, ranging from north to south temperate regions of the world. In these intertidal areas, the birds forage in mixed species assemblages on a variety of invertebrate prey. The majority of these shorebirds belong to two families, the Charadriidae (plovers) and the Scolopacidae (sandpipers), and although there is considerable dietary overlap between these groups, they differ in their foraging methods as well as in their morphology (Pienkowski 1979, Evans 1979). In intertidal habitats, the short-billed plovers all forage visually in a run-stop-search manner, whereby an individual pauses to search for prey before moving to capture a prey item or moving to search from a new position. Members of the sandpiper family, on the other hand, exhibit a variety of foraging techniques, foraging visually or tactilely, on mud or in water, and may even hunt fish in the manner of the Little Egret *Egretta garzetta* (Gutierrez & Dominguez 1991).

In this study, an inter-site comparison was made of the diet and foraging methods of a fixed-method forager, the Grey Plover (Charadriidae) and a versatile forager, the Whimbrel (Scolopacidae). Both are migratory species which occupy a broad range of latitudes during the nonbreeding season, and thus encounter a variety of foraging conditions. Aspects of the foraging ecology of Grey Plovers have been investigated at several sites in the northern hemisphere (e.g. Tees estuary, U.K. - Dugan 1980, 1982, Townshend 1982, 1985, Townshend, Dugan & Pienkowski 1984, Wood 1984; Lindisfarne estuary, U.K. - Pienkowski 1982, 1983; the Wash, U.K. - Dit Durell & Kelly 1990; New Haven, Connecticut - Baker 1974; Sanibel Island, Florida - Stinson 1977), but few data exist for the tropics and south temperate regions (Berg River estuary, South Africa - Kalejta 1991, Zwartkops estuary, South Africa - Schramm 1978, Martin 1991). Whimbrels are uncommon in the cold north temperate regions during the nonbreeding season, and although a few studies have been made of Whimbrels in the tropics (e.g. Panama - Mallory 1981, 1982; Guinea-Bissau - Zwarts 1985; Banc d'Arguin, Mauritania - Zwarts & Dirksen 1989, 1990, Zwarts 1990), studies from south temperate regions are few (Queule River estuary, Chile - Velásquez & Navarro 1993, Zwartkops estuary - Martin 1991).

The aims of this study were twofold:

1. To determine the amount and causes of variation in diet, foraging technique, energy intake rate, foraging time and foraging density at a range of different sites; and
2. To compare the amount of variability in these parameters for a fixed-method forager and a versatile forager.

METHODS

Study areas

Grey Plovers and Whimbrels were studied at nine sites ranging from equatorial east Africa to islands in the western Indian Ocean and mainland temperate South Africa (Table 4.1, Fig. 4.1). Data were collected at the same time of year as far as possible (i.e. mid to late austral summer).

Table 4.1. Location and characteristics of the nine study areas, listed in order of latitude from north to south.

Site	Total area (ha)	Study area (ha)	Study period	Characteristics
Mida Creek Kenya 03°22'S, 39°50'E	580	2.00	Mar '92	Predominantly sandy, undisturbed estuary, edged by mangroves and mud.
Mer Rouge Mauritius 20°08'S, 57°30'E	20	2.58	Feb '91	Muddy, polluted estuary, reclaimed to fraction of former size, heavily utilised by bait-diggers and fishermen.
Grande Rivière Noire Mauritius 20°22'S, 57°22'E	10	2.23	Feb '91	Small, lightly disturbed, muddy estuary fringed by invasive Guava trees.
Ile aux Benitiers Mauritius 20°25'S, 57°21'E	9	8.40	Feb '91	Undisturbed intertidal coral sandflat area on northern shore of small offshore island. Some muddier parts containing *Zostera*.
Passe de la Prairie Mauritius 20°28'S, 57°20'E		4.6	Feb '91	Small lightly disturbed estuary of sandy mud opening onto a vast intertidal area of coral sand. Birds concentrated in muddy mouth area with thick *Zostera* covering.
Tuléar Madagascar 23°23'S, 43°40'E	550	4.0	Feb '93	Muddy, sheltered intertidal area, moderately disturbed by bait-diggers and fishermen.
Berg estuary South Africa 32°47'S, 18°10'E	144	2.45	Apr '91	Predominantly muddy estuary with minimal disturbance.
Zwartkops estuary South Africa 33°52'S, 25°38'E	104	1.45	Mar '91	Predominantly muddy estuary, moderately disturbed by bait-diggers and fishermen.
Breede estuary South Africa 34°24'S, 20°50'E	150	1.3	Nov '91	Small, predominantly muddy estuary except near mouth, moderately disturbed by bait-diggers. Birds observed on a mixed sandy/muddy area with *Zostera*.

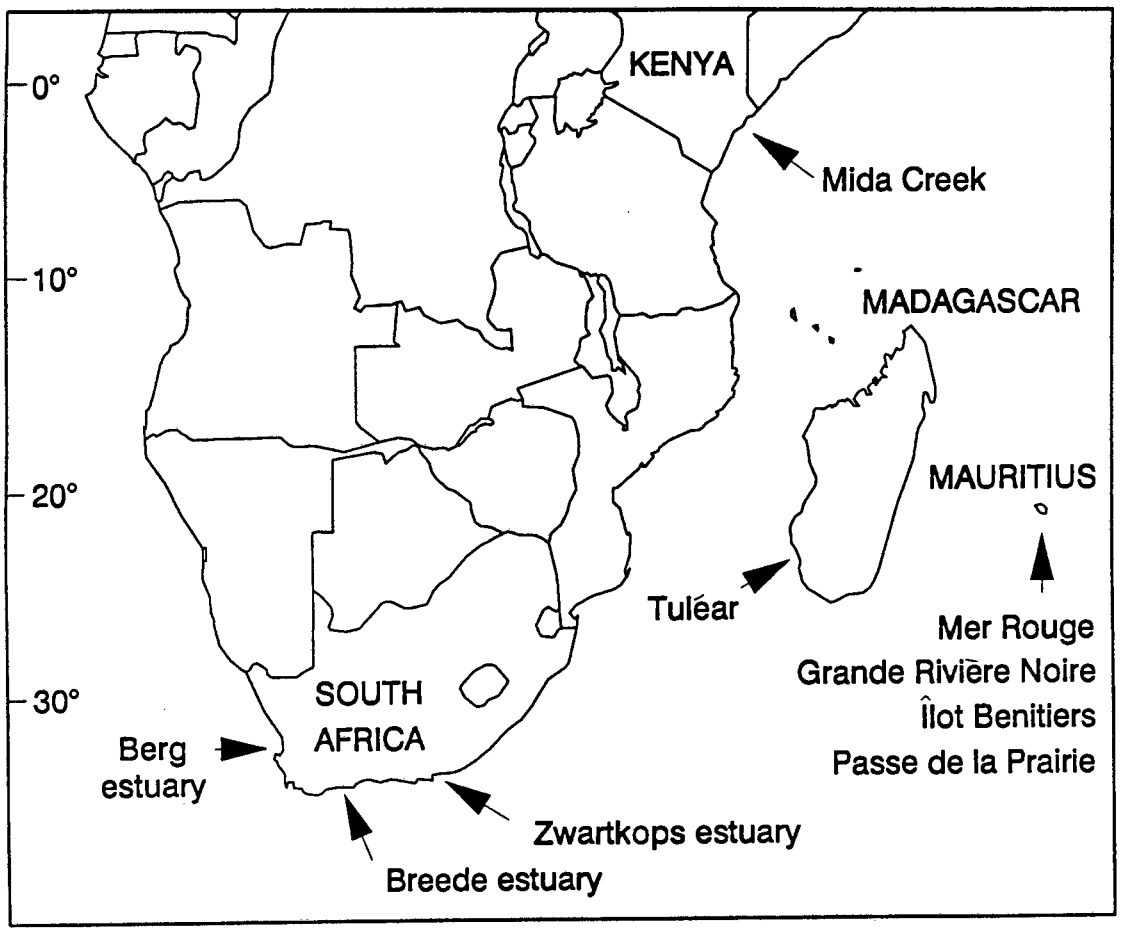


Figure 4.1. Location of the nine study sites.

Diet and foraging behaviour

Foraging behaviour was recorded during fixed-period focal observations of randomly-selected individuals. Sample duration was one minute for Whimbrels and 10 or 15 minutes for Grey Plovers, in order to record detailed aspects of their locomotion. During focal observations, the number of steps taken and pecks made were counted, and, in the case of Grey Plovers, the number of steps per foraging move ending in a searching pause or prey capture attempt were recorded separately. Habitat (water or mud) was noted for each observation. Grey Plover searching pauses were timed using a stopwatch. Prey were identified as far as possible and their size was estimated as a percentage of bill-length. The distance to the nearest conspecific neighbour was recorded when possible.

The terminology used in this chapter to describe foraging behaviour is clarified as follows:

Step rate - number of steps taken per minute;

Peck rate - number of pecks (successful and unsuccessful prey capture attempts) made per minute;

Prey capture rate - the total number of prey items swallowed per minute;

Move rate (Grey Plover only) - number of discrete foraging moves, ending either in a pause or prey capture attempt, made per minute;

Move length (Grey Plover only) - the number of steps per foraging move;

Search time (Grey Plover only) - the length of time (seconds) between stopping at the end of a foraging move and commencing the following move.

Energy intake rates

The accuracy of prey size estimates made in the field was tested using stuffed birds and simulated field conditions. Field estimates (E_f in mm) of crab sizes were calibrated using the equation, carapace width (mm) = 0.852 (E_f) + 4.713 (n = 75, r = 0.94) for Grey Plovers, and carapace width (mm) = 0.787 (E_f) + 2.720 (n = 98, r = 0.91) for Whimbrels. Prawn size estimates were calibrated using the equation, total length (mm) = 0.67 (E_f) + 20.4 (n = 50, r = 0.88) for Grey Plovers, and total length (mm) = 0.64 (E_f) + 18.9 (n = 232, r = 0.86) for Whimbrels.

Crabs, prawns and polychaete worms were collected in the field, dried, weighed, and energy content per dry mass was determined by bomb calorimetry. The equations used to calculate gross energy content of prey are listed in Table 4.2. Assimilation efficiencies of 65% for crabs (Zwarts & Blomert 1990), 70% for prawns (Chapter 1) and 85% for polychaete worms (Gibb 1957) were used to calculate net energy intake.

Table 4.2. Equations used to convert body measurements (CW = carapace width, CL = carapace length, TL = total length, JL = jaw length) in mm to dry mass (DM, in g), and the energy content (kJ) per unit dry mass.

Prey species	Conversion to dry mass (g)		kJ/g dry mass
Small polychaetes (Mida)	$DM = 3.94 \times 10^{-5}(TL)^{1.44}$	($n = 71$, $r = 0.63$)	11.69
Ceratonereis sp.	$DM = 4.57 \times 10^{-6}(JL)^{2.79}$ $TL = 60.63(JL) - 11.31$	($n = 20$, $r = 0.72$) ($n = 35$, $r = 0.82$)	17.60
Marphysa sp.	$DM = 1.68 \times 10^{-5}(TL)^{2.05}$	($n = 26$, $r = 0.93$)	13.48
Thalamita admete	$DM = 1.45 \times 10^{-5}(CW)^{3.557}$	($n = 63$, $r = 0.93$)	8.393
Uca marionis	$DM = 7.16 \times 10^{-5}(CW)^{3.10}$	($n = 43$, $r = 0.90$)	9.212
Dotilla fenestrata	$DM = 6.09 \times 10^{-5}(CW)^{3.29}$	($n = 93$, $r = 0.98$)	11.32
Cleistostoma spp	DM = 0.054g (mean)	(Martin 1991)	14.86
Upogebia africana	$DM = 7.2 \times 10^{-5}(CL)^{3.152}$ $TL = 3.094(CL) - 0.348$	(Martin 1991)	14.49
Callianassa sp.	$DM = 1 \times 10^{-6}(TL)3.45$	($n = 29$, $r = 0.93$)	16.32
Solen cylindricus	$DM = 5.05 \times 10^{-6}(TL)^{2.70}$	($n = 27$, $r = 0.97$)	19.52

Densities and foraging time

At each study area (except Tuléar), the number and activity (foraging [including aggression] or resting) of Grey Plovers and Whimbrels were recorded at half hour intervals throughout the low tide period over a minimum of two days. Average foraging and total densities on the study areas were calculated as the mean of all respective counts during the period when low tide exposure was at least 50%.

Foraging time (*FT*, minutes) was calculated using the equation,

$$FT = \Sigma_{ti..n}(F_{ti}/F_{max}.I),$$

where F_{ti} is the number of birds foraging at the ith count, F_{max} is the maximum number foraging during low tide, and I is the count interval in minutes.

RESULTS

Diet

Grey Plovers ate both polychaetes (e.g. *Marphysa*, *Nereis*) and crabs (e.g. *Thalamita*, *Macropthalmus, Dotilla*) in roughly equal proportions at all of the tropical sites (Fig. 4.2), in addition to a fairly large proportion of small unidentified prey. At the Zwartkops estuary, the percentage of polychaetes (*Ceratonereis*) in the diet was low, and Grey Plovers took mainly crabs (*Cleistostoma*) and prawns (*Upogebia*); at the

Breede estuary their diet also included a substantial proportion of prawns (*Upogebia*). At the Berg estuary, the only site outside the Indian Ocean, the diet comprised mainly polychaetes (*Ceratonereis*), and a few crustaceans (*Upogebia* and *Hymenosoma*) were also taken. Grey Plovers took a small proportion of bivalves (*Solen*) at Mida Creek. At the Zwartkops estuary, *Solen* remains discarded by other species (such as African Black Oystercatcher *Haematopus moquini*) were eaten occasionally. Small unidentified prey items were prominent in Grey Plover diets, particularly at the Berg estuary. These items are likely to have included polychaetes, because the latter were usually consumed very rapidly, and the probability of noticing only the swallowing action was thus high. An analysis of Grey Plover droppings from the Berg estuary by Kalejta (1991) confirmed the dominance of polychaetes in the diet, but also yielded fragments of isopods *Exosphaeroma hyloecetes* in 22% of samples. At the Zwartkops estuary, Martin (1991) also recovered crabs *Thaumastoplax spiralis*, dipterids (*Lonchoptera*) and gastropods (*Assiminea bifasciata*) from Grey Plover stomachs.

At most sites, more than 95% of the prey taken by Whimbrels were crabs (*Thalamita, Macropthalmus, Uca, Dotilla, Hymenosoma* and *Cleistostoma*), and polychaetes were seldom eaten. At the Zwartkops estuary, however, prawns and crabs were eaten by Whimbrels in approximately equal numbers (Fig. 4.2). Whimbrels at the Zwartkops estuary consume *Sesarma catenata* crabs in the saltmarshes at high tide (pers. obs.), but the amount of *Sesarma* in the diet could not be quantified, and is not included in Fig. 4.2. In addition, both Grey Plovers and Whimbrels opportunistically consumed small fish at several sites when these were stranded in pools.

Crabs contributed most (> 50%) to the net energy intake of Grey Plovers and Whimbrels at tropical and subtropical sites, but contributed on average far less to their energy intake at temperate South African sites (Fig. 4.2).

The size of prey taken by Grey Plovers differed very little between sites (Fig. 4.3), with at least 75% of prey falling into the smallest size class (< 0.125g dry mass) at all sites. Larger crabs were taken in roughly equal proportions at Mida Creek, the sites in Mauritius, and Tuléar, whereas prawns dominated the large prey at the Zwartkops and Breede estuaries. At the Berg estuary, very few large prey were taken, and these were all prawns. Whimbrels took a greater proportion of large prey than Grey Plovers, although 39 - 86% of their prey were smaller than 0.125g dry mass (Fig. 4.3).

Prey size differed significantly between sites for both Grey Plovers and Whimbrels (Kruskal-Wallis One-way Analysis by Ranks, H = 1452.6 and 105.0 respectively, both $P < 0.001$). Although both species consumed crabs and prawns larger than 3g dry mass, Grey Plovers took small prey more frequently than Whimbrels (Wilcoxon test, $U = 40.39$, $P < 0.001$).

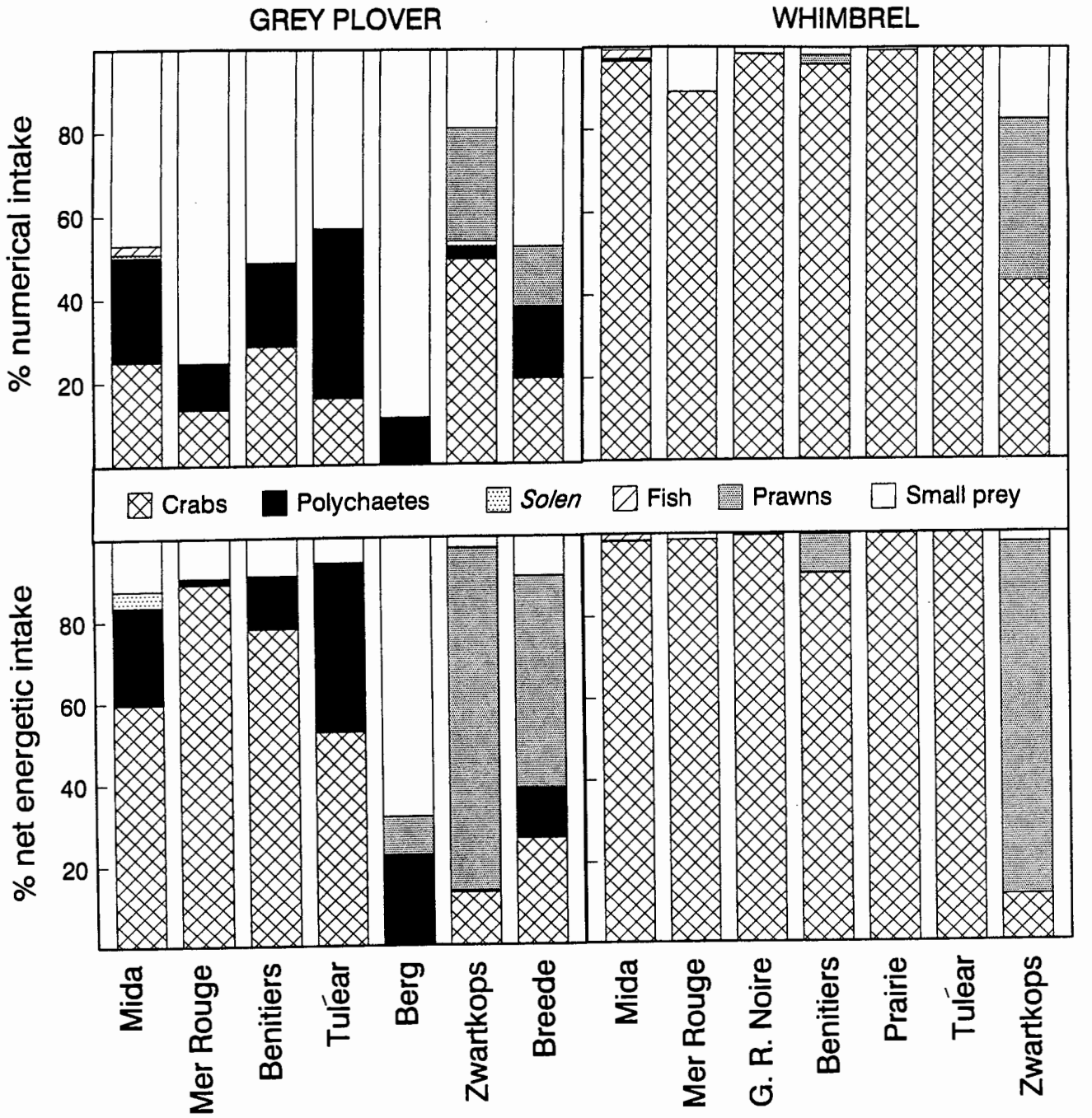


Figure 4.2. Percentage numerical and energetic contribution of different prey types to the diet of Grey Plovers and Whimbrels at the different study sites. Sample sizes of prey are the same as in Fig. 4.3.

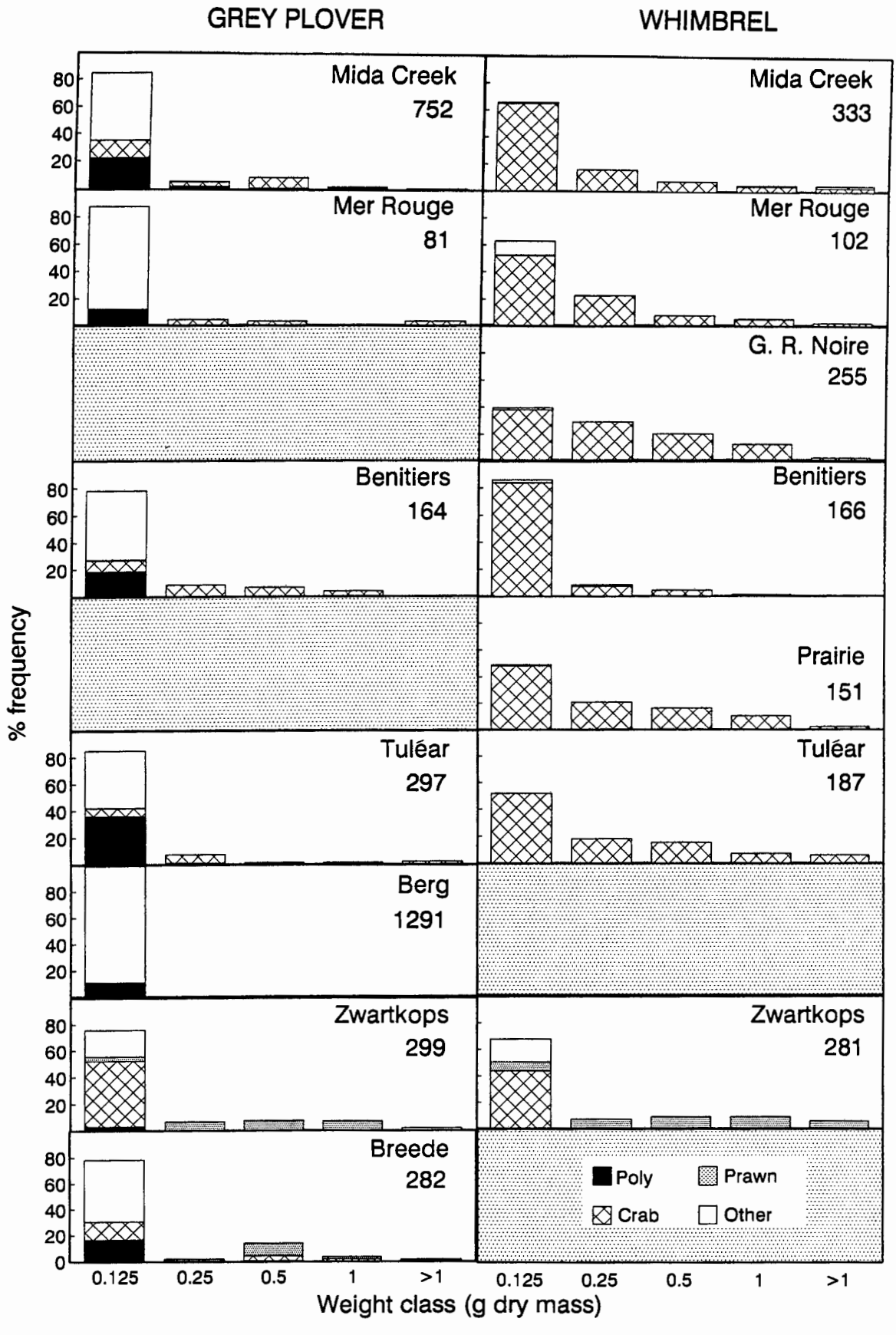


Figure 4.3. Percentage frequency of different size classes of prey in the diets of Grey Plovers and Whimbrels at the different study sites.

Table 4.3. Intercorrelations (r) between Grey Plover foraging parameters (all n.min^{-1}, except move length - steps/move, search time - s); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Step rate	Peck rate	Move length	Move rate	Prey capture rate
Peck rate	n.s.				
Move length	0.87*	-0.81*			
Move rate	n.s.	0.93**#	n.s.		
Prey capture rate	-0.84*	0.96***	n.s.	n.s.	
Search time	n.s.	n.s.	n.s.	n.s.	n.s.

Excluding the Berg estuary.

Grey Plover foraging technique

Grey Plovers foraged visually, in a run-stop-search manner at all the sites, each foraging move ending in a search pause or prey capture attempt. The modal move length was two or three steps at all of the sites, but the frequency with which longer moves were made differed between sites (Fig. 4.4). The proportion of moves of 10 or more steps was low in most areas, but was more than 10% at Mer Rouge and Grande Rivière Noire, and was nearly 30% at the Zwartkops estuary. In general, prey were captured over distances of 1 to 3 steps, but at the Zwartkops estuary, prey frequently were captured over distances of 10 steps or more (Fig. 4.4).

The modal time spent searching for prey between foraging moves was 2 or 3 seconds at most sites (Fig. 4.4). Pauses of 10 seconds or more were most common at Mida Creek and Mer Rouge, and the average pause duration was significantly longer at Mer Rouge, Mida Creek and Ile aux Benitiers than at the other sites ($ANOVA_{6,2538}$, $P < 0.001$, Tukey test). Several foraging parameters were intercorrelated (Table 4.3).

Peck and numerical prey intake rates were negatively correlated with the percentage of prey greater than 0.5g dry mass in the diet ($n = 7$, $r = -0.86$, $P < 0.05$, and $n = 7$, $r = -0.92$, $P < 0.01$ respectively), and step rate was negatively correlated with the percentage of small prey in the diet (< 0.25g dry mass) except at the Breede estuary, where both step rate and the percentage of small prey were low ($n = 6$, $r = -0.97$, $P < 0.01$).

There were no significant relationships between the coefficient of variance in any foraging parameter and the diversity of prey types or sizes taken.

Step rate ($n = 7$, $r = 0.81$, $P < 0.05$) and move length ($n = 7$, $r = 0.83$, $P < 0.05$) were positively correlated with the proportion of large crustaceans (crabs and prawns) in the diet (Fig. 4.5). The proportion of large crustaceans in the diet was negatively related to peck rate ($n = 7$, $r = -0.85$, $P < 0.05$) and prey intake rate ($n = 7$, $r = -0.82$, $P < 0.05$; Fig. 4.5). The average duration of search pauses and the proportion of long pauses ($\geq$10 s) were not related to any other variables, but average pause time was shortest at sites dominated by either the smallest or largest prey

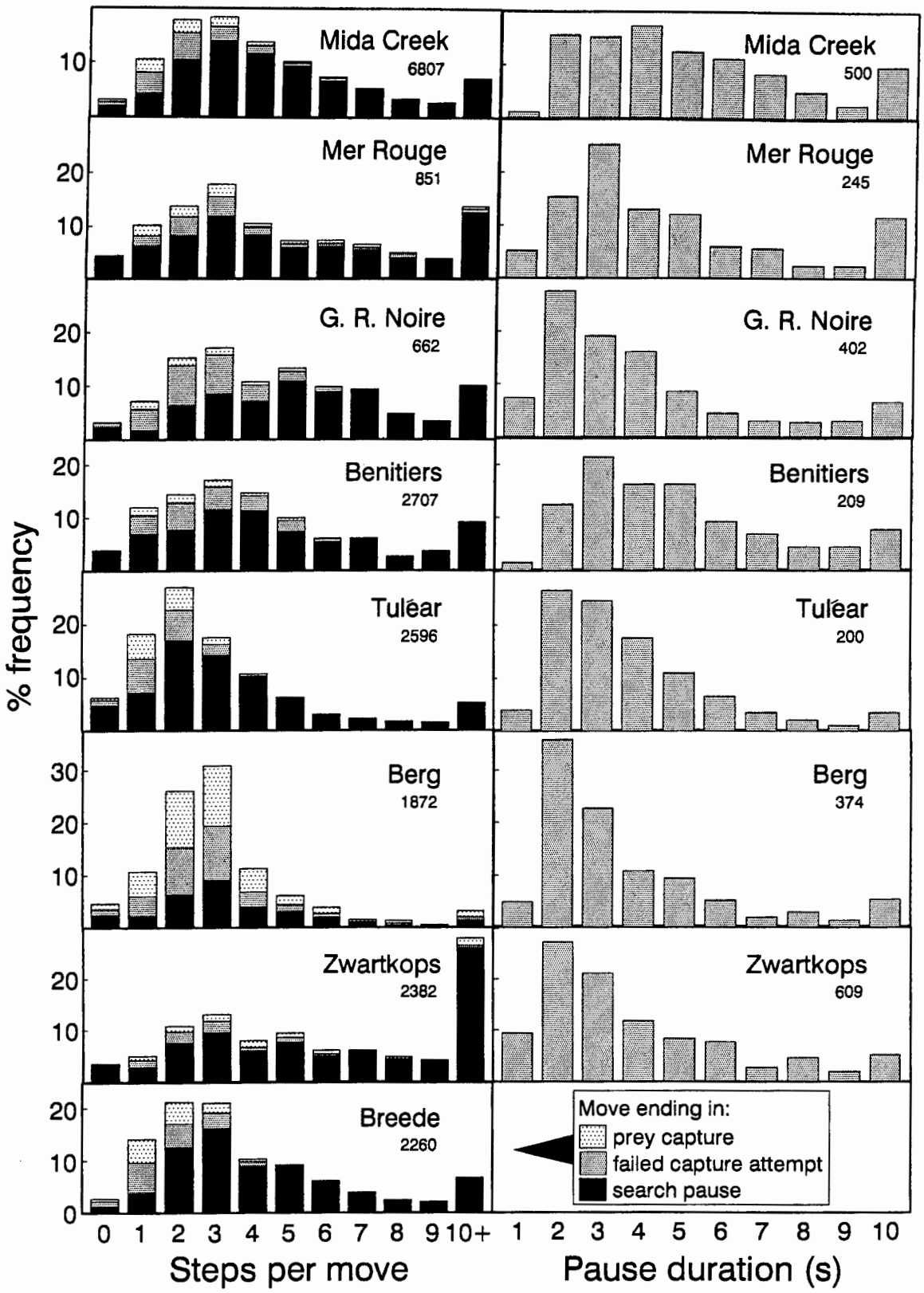


Figure 4.4. Percentage frequency distribution of the number of steps made per foraging move and the duration of search pauses by Grey Plovers for each of the study sites.

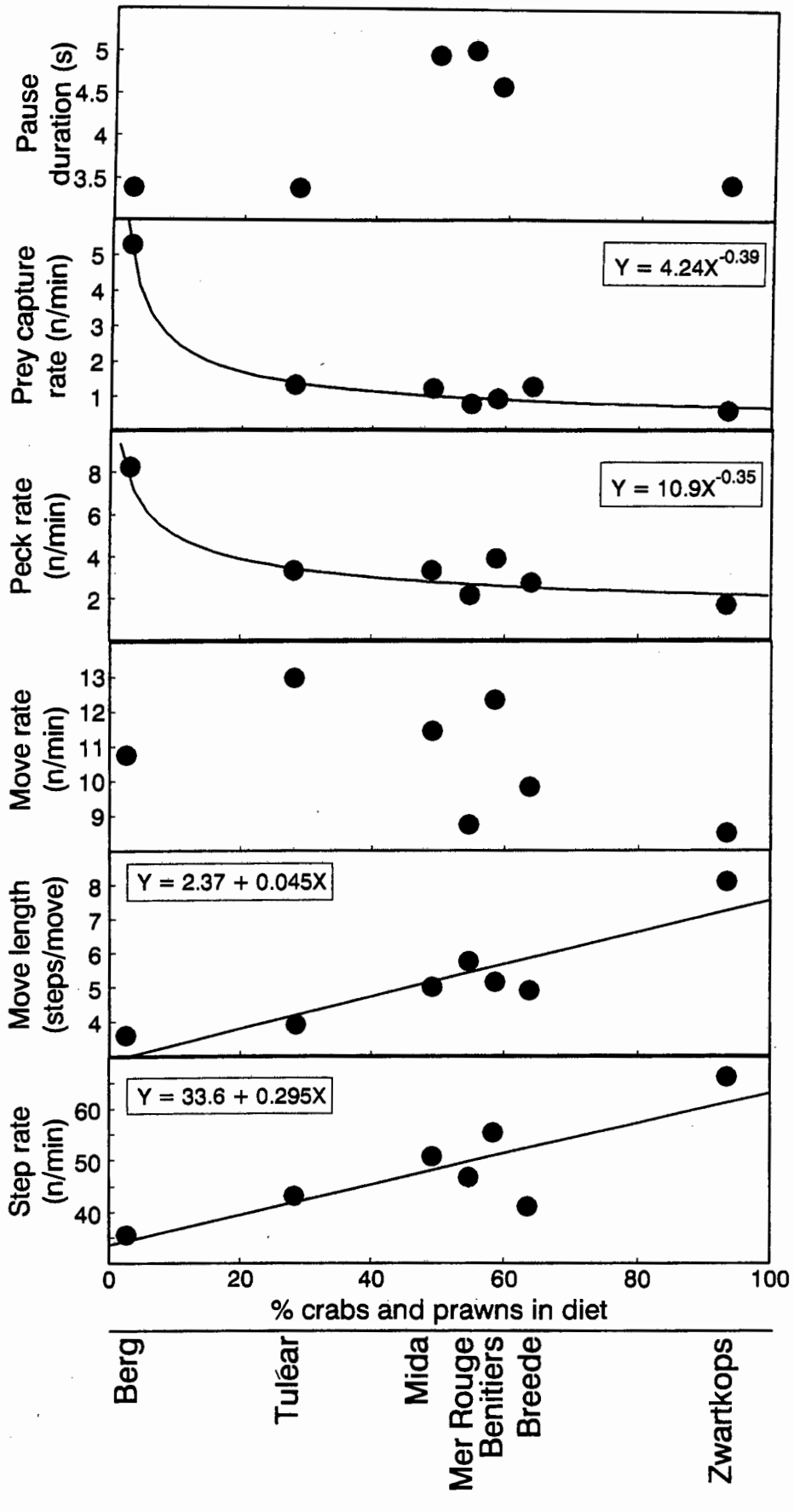


Figure 4.5. Relationships of different foraging parameters to the percentage of large crustaceans (crabs and prawns) in the diet of Grey Plovers at the different sites.

types (Fig. 4.5). Move rate of Grey Plovers is affected by peck rate, search rate and duration, move length and running speed, and did not show any detectable trends in relation to prey type or size. Move rate did not vary much between most sites (Fig. 4.5), implying that longer moves were executed at greater speed. However, move rate was much higher at Grande Rivière Noire than the other sites. At Grande Rivière Noire, Grey Plovers chased fiddler crabs over intermediate distances (move length) but with high speed and frequency.

Whimbrel foraging technique

Whimbrels walked continuously whilst foraging, but walking speed ranged from a few steps to over 200 steps per minute, and peck rate was also highly variable. Prey capture rate was unrelated to peck rate. When foraging tactilely, step rates were low and peck rates high, as illustrated at Passe de la Prairie, where Whimbrels spent most of their time foraging in submerged *Zostera* beds (Fig. 4.6). At Ile aux Benitiers, foraging on mud was mostly tactile, but in water Whimbrels foraged using both tactile and visual methods, as illustrated by the bimodal distribution of step to peck ratios. At the Zwartkops estuary, step rates were usually high, and peck rates low, and Whimbrels foraged almost entirely visually, including in water. At Mer Rouge Whimbrels also foraged predominantly visually both on mud and in water, but at Tuléar, foraging was predominantly tactile on mud and visual in water. At Mida Creek and Grande Rivière Noire, nearly all foraging was on exposed substrates, and was visual.

Densities

The overall densities of both Grey Plovers and Whimbrels were highest at the Zwartkops estuary (Table 4.4). Because the overall densities also take least preferred habitats into account, densities of actively foraging birds were always higher than the overall densities. Whimbrel foraging densities were higher than one bird.ha^{-1} at all the sites except the Breede estuary, and Grey Plover densities were lower than one bird.ha^{-1} at two sites, Grande Rivière Noire and Passe de la Prairie. The average nearest-neighbour distances maintained by foraging Grey Plovers varied little, ranging between 17 and 24 metres. Whimbrel nearest-neighbour distances were far more variable (Table 4.4) and, with the exception of Passe de la Prairie, where overall foraging densities were low but Whimbrels foraged tactilely in close proximity, nearest-neighbour distances were negatively correlated with foraging density (n = 5, r = -0.96, $P < 0.01$). Apart from a negative correlation with Grey Plover move rate (n = 7, r = -0.87, $P < 0.05$) the density of foraging birds was not significantly related to any measured foraging parameter for either species.

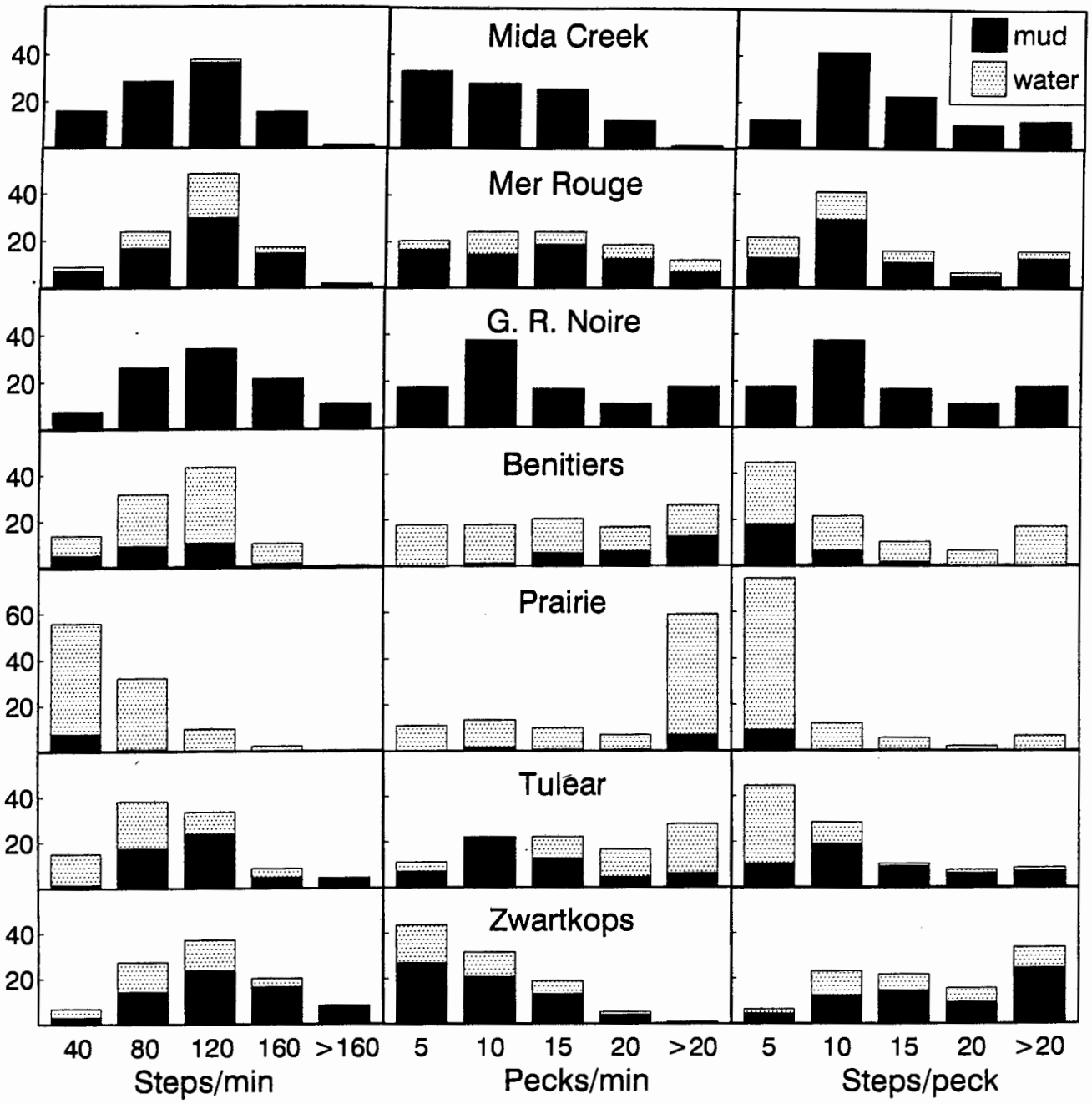


Figure 4.6. Frequency distributions of step and peck rates and the ratio of steps to pecks in different habitats (water and mud) for Whimbrels at the different sites.

Table 4.4. Duration of low tide exposure (h), focal sample size (min), net energy intake rate (kJ/min), mean foraging time per low tide period (min), percentage of exposure time spent foraging, total daytime intake (kJ), foraging density (mean number foraging on study area), average distance to nearest-neighbour (m) and overall density (total number/total intertidal area) of Grey Plovers and Whimbrels at the different sites.

Site	Exposure time (h)	*n* (min)	Net intake rate (kJ/min)	Foraging time (min)	%	Total daytime intake (kJ)	Foraging density (n/ha)	Nearest neighbour (m)	Overall density (n/ha)
GREY PLOVER									
Mida Creek	9	616	0.79	325	60	257	4.4	20.9	1.46
Mer Rouge	6-7	104	0.69	250	64	173	5.6		2.50
G. R. Noire	5-6						0.6		
Benitiers	5-6	193	0.53	219	66	116	2.2	23.8	
Prairie	4-5						0.3		
Tuléar	4-5	200	1.20				<4*		0.41
Berg	6-7	226	0.88	241	62	212	7.3	17.1	2.17
Zwartkops	3.5-5	566	1.16	186	73	216	6.8	20.8	5.80
Breede	5-6	235	1.38	228	69	315	6.4	18.7	
WHIMBREL									
Mida Creek	9	497	1.70	283	52	481	1.7	56.7	0.51
Mer Rouge	6-7	240	0.68	272	70	185	6.2	25.1	3.55
G. R. Noire	5-6	214	1.77	229	69	405	1.4	96.1	
Benitiers	5-6	224	0.67	230	70	154	9.7	10.2	
Prairie	4-5	205	1.16	167	62	194	2.9	10.8	
Tuléar	4-5	172	1.83				<4*		1.10
Berg	6-7						2.6		0.34
Zwartkops	3.5-5	1258	1.29	162	64	209	12.1	18.1	4.51
Breede	5-6						0.4		

* estimated

Foraging time and energy intake

The lowest energy intake rates for both Grey Plovers and Whimbrels were recorded at two Mauritian sites, Mer Rouge and Ile aux Benitiers. Observation at both of these sites was difficult due to the distances involved, so it is possible that intake rates were underestimated. Apart from these sites, energy intake rates varied between sites by up to 1.7 times (Table 4.4). Neither Grey Plover nor Whimbrel energy intake rates were significantly related to any recorded parameters of foraging effort or prey size, but Grey Plover intake rates tended to be highest at sites where foraging density was high.

Both Grey Plovers and Whimbrels foraged for approximately 60 to 75% of the duration of low tide exposure, except at Mida Creek, where the mudflats were exposed for two hours longer than at any other site, and Whimbrels foraged for only 52% of the exposure period (Table 4.4). In addition, both Grey Plovers and Whimbrels were seen foraging at night at all the sites that were visited at night (all but Grande Rivière Noire and Tuléar). Neither daytime foraging time (Grey Plover: $n = 6$, $r = 0.32$; Whimbrel: $n = 6$, $r = 0.01$) nor the percentage exposure time for which Grey Plovers ($n = 6$, $r = 0.59$) and Whimbrels ($n = 6$, $r = -0.57$) foraged was related to energy intake rates.

DISCUSSION

Intraspecific variability in diet, foraging behaviour and success

Diet

Most migratory waders prey upon a variety of prey types in their intertidal foraging areas (Cramp & Simmons 1983), the maximum sizes of which are limited by the width of their gapes (e.g. Zwarts 1985). Both Grey Plovers and Whimbrels consumed a variety of prey species both within and between the different sites in this study. However, dietary compositions reflected specialist tendencies for Whimbrels, which ate almost exclusively crabs at most sites.

In north temperate regions, Grey Plover diets are dominated by worms and other small species, and Baker (1974) suggested that their stereotyped foraging behaviour was linked to a specialized diet of worms. Dominant prey eaten at various sites in the U.K. include *Arenicola*, *Notomastus*, *Scoloplos*, *Nereis, Lanice, Corophium,* and *Hydrobia* (Goss-Custard, Jones & Newbery 1977a, Pienkowski 1982, Dit Durell & Kelly 1990). *Nereis* dominates the diet in the Netherlands (Kersten & Piersma 1984) and Connecticut (Baker 1974), and *Nereis* and *Cerebratulus* worms are eaten in the Bay of Fundy, Canada (Hicklin & Smith 1979). Grey Plover diets are dominated by polychaete worms in South Korea, but they were also recorded (with surprise) to eat bivalves *Solen strictus* and crabs (Piersma 1985). In Guinea-Bissau, Grey Plover diets include fiddler crabs *Uca tangeri* (Zwarts 1985), and in Mauritania, barnacles make up a large proportion of prey (Piersma 1982). At the tropical and south temperate sites in this study, Grey Plover diets were fairly diverse, both within and between sites. In addition to polychaete worms and other small prey, including small gastropods, isopods and insects, Grey Plovers at these sites consumed a relatively large proportion of larger prey species, including several crab species, mudprawns, bivalves and stranded fish. Thus the composition of Grey Plover diets reflects the regional availability of prey types, with a higher proportion of large prey consumed in the tropics and south temperate regions than in north temperate regions.

Both Grey Plovers and Whimbrels included a large proportion of prawns in their diets when these were available. *Upogebia* occurred at high densities at the Zwartkops estuary (average $218.m^{-2}$, Hanekom *et al.* 1988) and the Breede estuary (up to $400.m^{-2}$ in certain areas, Day 1981), where they formed an important part of the diet for both species. *Upogebia* at the Zwartkops estuary are frequently active close to the surface and sometimes leave their burrows at low tide. This behaviour, thought to be induced by parasites, increases the availability of larger size classes of *Upogebia*

(which normally remain in their burrows at low tide) to visually-foraging birds. Whether the *Upogebia* at the Breede estuary exhibit the same surfacing behaviour is unknown, but frequent disturbance by bait diggers brings prawns to the surface at this site (pers. obs.). Because of their large size, greater digestibility, and relatively high profitability, prawns are likely to be taken by both Grey Plovers and Whimbrels whenever they are encountered. However, Grey Plovers took longer than Whimbrels to handle large mudprawns, which they broke apart before swallowing; they also rejected very large mudprawns more frequently than Whimbrels. Mudprawns also occurred at the Berg estuary, but at densities of only 25 *Callianassa* and 1.6 *Upogebia* per m^2 (Kalejta & Hockey 1991), and were infrequently taken by Grey Plovers. Mudprawns did not occur at Mida Creek (pers. obs.), and only one was caught by a Grey Plover at Tuléar. *Callianassa* were eaten occasionally by Whimbrels in Mauritius.

Whimbrel diets were dominated by large crustaceans in this study, but a variety of species, with different habits and occurring in different microhabitats, were taken, depending on their availability at different sites. It has been suggested that Whimbrels' bill morphology evolved to facilitate probing into curved crustacean burrows (Mallory 1981), and most studies indicate crabs to be the main prey of Whimbrels (Gunther 1963, Ali & Ripley 1969, Summers 1980, Mallory 1981, Myers, Maron & Sallaberry 1985, Piersma 1985, Zwarts 1985, Zwarts & Dirksen 1990). However, Whimbrels do eat large polychaetes as a main prey type at sites where large crustaceans are rare or unavailable (e.g. southern Chile - Velásquez & Navarro 1993).

Foraging technique

Grey Plovers did not deviate from their stereotypic visual foraging method at any of the sites. Whimbrels, on the other hand, foraged both visually and tactilely at all sites, although one or the other method was usually dominant at each site. In addition to walking continually while foraging, Whimbrels also used a 'stand and wait' method at Mer Rouge, Grande Rivière Noire, Tuléar and Mida Creek, a behaviour which has also been recorded at the Banc d'Arguin for Whimbrels capturing *Uca* (Zwarts 1990). Moreover, whereas Grey Plovers seldom foraged in water, except occasionally on the incoming or outgoing tide, Whimbrels frequently made use of this habitat, even when the tide was out.

Despite their stereotypic foraging method, however, Grey Plovers were able to change the emphasis of various components of this behaviour in response to the relative availability of different prey types, resulting in variation in their overall foraging technique between sites. This was clearly illustrated by the differences in foraging behaviour at the Zwartkops and Berg estuaries where prey intake was dominated by

large crustaceans and polychaetes respectively. Grey Plovers at the Zwartkops estuary foraged rapidly, having long move lengths and rapid step rates, whereas at the Berg estuary they made very short, slow, moves and took few steps per minute. Foraging speed was intermediate at those sites where the relative abundance of crabs and polychaetes was more even, such as Mida Creek and Mer Rouge. These trends in both move length and step rate could probably be explained by the relative densities of polychaetes and crustaceans and the distances at which the different prey types can be detected. Grey Plovers have been found to search increasingly large areas (suggested by longer distances per foraging move) as prey availability decreases with the receding tide (D.J. Townshend in Evans 1979) or decreasing temperatures (Pienkowski 1983).

The distance moved between searching for prey is indicative of the area searched, and may be limited by the range of prey detection, or the distance within which a bird can capture prey while it is still available (Pienkowski 1983). The distance travelled to capture prey was shorter than when moving to a new searching position (Fig. 4.4), as has been demonstrated previously (Baker 1974), because prey are captured within the area searched. In addition, successful pecks have been found to be followed by shorter moves than unsuccessful pecks (Baker 1974), and the distance moved is inversely related to the energetic value of the prey item (Pienkowski 1981). This reaction is an adaptation to remaining in or locating richer areas as the need may be.

Baker (1974) found that the length of time between catching prey items was shorter when Grey Plovers were foraging on two prey types rather than one. In this study, the opposite trend occurred for the length of time for which Grey Plovers stopped to search for prey, as pause duration was shortest at the sites where prey were dominated by either large crustaceans or polychaetes. Because of their size, crabs and prawns could be spotted quickly and from long distances. Polychaete activity, on the other hand, may be suppressed after a bird's presence is detected (Esselink & Zwarts 1989), causing a rapid decrease in the benefit of searching from a stationary position. In addition, because most polychaetes were captured over very short distances, Grey Plovers probably only had to search a small area, which could be done rapidly. The longer duration of search pauses at the sites where Grey Plovers had a mixed diet may be because the birds were unable to develop a focused search image. Grey Plovers foraging on large and small polychaete worms at Lindisfarne estuary were found to have shorter pause times before catching larger than smaller worms, and it was argued that birds become decreasingly selective of worm size during the search pause (Pienkowski 1981).

Whimbrel foraging behaviour could not be broken down into component movements. Their foraging behaviour showed a continuum from slow, tactile foraging

to fast visual foraging, the former usually occurring in water and the latter extreme being reached at sites with large, surface-active prey (e.g. fiddler crabs). Whimbrels change their walking and pecking speed as sediment type and water depth changes, either spatially or temporally (e.g. Velásquez & Navarro 1993), and frequently changed from visual to tactile methods within a one-minute focal observation. Both on mud and in water, Whimbrels foraged visually when hunting surface-active prey (e.g. Zwartkops estuary), and tactilely when crabs were hidden amongst *Zostera* (e.g. Passe de la Prairie and Tuléar). In heterogenous sites, Whimbrels frequently moved between habitats and switched between visual and tactile methods, probably in response to changes in prey availability and prey capture rates. However, the fact that Whimbrels even search visually for worms when substrate conditions allow (Velásquez & Navarro 1993) suggests that visual foraging is the preferred method whenever visual cues exist.

Foraging densities, energy intake rates and foraging time

The hypothetical carrying capacity of an estuary will be such that birds foraging maximally will achieve the minimum energy intake rate required to satisfy their energy requirements within the foraging time available. Thus, in such a resource-limited situation, foraging densities ultimately will be limited by the amount of foraging space required by individuals to achieve this minimum intake rate. Ideally, if resources are limited to a similar degree at different sites, foraging time may be expected to be a relatively constant proportion of the time during which prey are available.

The generally low foraging densities and similarity in nearest-neighbour distances for Grey Plovers at different sites, and the highly variable densities of Whimbrels at different sites, largely reflected the different spatial requirements of visual and tactile foraging methods.

Grey Plover foraging densities varied little between most sites, but were much lower at Passe de la Prairie, Grande Rivière Noire and Ile aux Benitiers. The *Zostera* beds at Passe de la Prairie supported a high density of crabs (pers. obs.), but these were mostly hidden amongst the *Zostera*, and thus the proportion available to visual foragers would have been low. In addition, these beds were always immersed, and the area shallow enough to forage in would have been more limited for Grey Plovers than Whimbrels. During neap tides, waders did not utilise this area at all, as *Zostera* beds were too deeply submerged. Grey Plovers at Grande Rivière Noire appeared to experience extreme difficulty in catching the rapidly moving fiddler crabs, reflected in the low proportion of successful prey capture attempts at this site (Fig. 4.4). The low foraging densities of Grey Plovers at Ile aux Benitiers were mainly due to the small area of muddy sediment which occured between areas of coarse coral sand, the latter being largely avoided by the Grey Plovers. Similarly the low density of Whimbrels at

the Breede estuary, was due to their foraging activity (on mudprawns) being mainly restricted to a small, muddy, *Zostera*-covered part of the study area.

Whimbrel densities were low throughout Grande Rivière Noire, where they held large territories. The density of fiddler crabs was visibly very high at this site, but foraging birds were always surrounded by a large barren halo caused by fiddler crabs retreating into their burrows. The response of this halo was always very rapid in relation to the movement of a bird, thus forcing the birds to resort to high speed dashes in an attempt to capture the crabs before they retreated. Under these circumstances, a higher density of foraging birds would not only reduce the availability of crabs, but would hamper their attempts to capture them. At Mida Creek, Whimbrels spread out evenly over the sandflats, resulting in the low foraging densities there. Although crab activity was visible on the surface at this site from a distance, their densities did not appear to be high, and the undulating nature of the substrate at this site probably further reduced the effective visibility of these prey, resulting in the large areas required by Whimbrels in which to forage. Whimbrel densities were very low at the Berg estuary despite the high density of *Hymenosoma* crabs there ($85.m^{-2}$, Kalejta & Hockey 1991), but this was possibly due to the small size of these crabs (B. Kalejta, pers. comm.).

Whimbrels foraged at high densities at Passe de la Prairie and Ile aux Benitiers, where foraging was predominantly tactile, and their nearest-neighbour distances were particularly low, due to the small spatial requirements of this foraging method. However, their densities were also high at the Zwartkops estuary, despite their predominantly visual foraging habits at this site. These densities were most likely to have been possible because of their use of saltmarsh habitats to supplement their intake at mid tide levels (Chapter 1). The high densities of both Whimbrels and Grey Plovers relative to their low energy intake rates at Mer Rouge may have been partly caused by the habitual return of individuals to the site despite recent major reductions in intertidal area due to reclamation, coupled with high pollution levels and frequent disturbance by people and feral dogs.

Both Grey Plovers and Whimbrels foraged for a fairly constant proportion of tidal exposure duration at most sites, which suggests that birds may have been making full use of available foraging time within digestive constraints. Although energy intake rates were frequently higher at sites where tidal exposure was shorter, there were several deviations from this trend, but these are discussed below.

According to allometrically-based predictions (Chapters 1, 3), Grey Plovers' daily energy requirements are *ca.* 400 $kJ.day^{-1}$ and Whimbrels' requirements exceed 600 $kJ.day^{-1}$ (see Chapters 1 and 3) during the premigratory period. Both species foraged throughout the diurnal and nocturnal low tide period at the Zwartkops estuary (where the tidal exposure period was shortest) in order to meet these requirements

(Chapter 3). Intake rates were similar to those at the Zwartkops estuary for Grey Plovers at Tuléar and for Whimbrels at Passe de la Prairie, where tidal exposure duration was similar. Whimbrels at Tuléar and at Grande Rivière Noire had the highest energy intake rates, and could satisfy a relatively large proportion of their energy requirements during the daytime alone. However, fiddler crabs dominated the diet at both these sites, and may be less active or more difficult to capture at night. Whimbrels eating fiddler crabs in Mauritania achieved only 17 - 58% of their daytime intake rates at night (Zwarts & Dirksen 1990).

Similarly, the very low energy intake rates of Grey Plovers and Whimbrels at Ile aux Benitiers and Mer Rouge may have been compensated by higher prey availability and intake rates at night (e.g. Dugan 1981), when their numbers at both sites were at least as high as during the day (unquantified obs.). If the calculations of energy intake rates at these sites were accurate, neither species at Mer Rouge or Ile aux Benitiers could achieve their daily energy requirements by foraging for as long at night as by day, if it is assumed that energy intake rates were the same at night (see Chapter 3). However, the body weights of adult Grey Plovers and Whimbrels exceeded their lean mass, calculated from wing length (Zwarts *et al.* 1990c), both at Mer Rouge and Ile aux Benitiers (Grey Plover - Mer Rouge: 220.7 ± 17 (S.D.) g, lean mass 191 ± 7 g, n = 3; Ile aux Benitiers: 224.4 ± 23 g, lean mass 183 ± 8 g, n = 5; Whimbrel - Mer Rouge: 420.5 ± 23 g, lean mass 402 ± 32 g, n = 4; Ile aux Benitiers: 444.5 ± 49 g, lean mass 402 ± 26 g, n = 18). This suggests that the birds achieved the balance of their requirements at night or by foraging elsewhere. Both species defended fixed territories at Mer Rouge, so it is unlikely that these birds supplemented their energy intake elsewhere. Grey Plovers and Whimbrels moved between Ile aux Benitiers and other mainland sites, including Passe de la Prairie, and the former was a major evening high-tide roost site for both species. Thus birds may have foraged at other sites in addition to Ile aux Benitiers.

The high energy intake rate recorded for Grey Plovers at the Breede estuary was probably partly due to the fact that the study was conducted early in the summer (November); energy intake rates at the Zwartkops estuary were maximal during spring and decreased during summer (Chapter 1).

Grey Plovers had fairly low energy intake rates at Mida Creek, where tidal exposure period was the longest, but Whimbrel intake rates were fairly high, and they foraged for only half of the available time. This could indicate that food was not a limiting factor for Whimbrels at this site, but the fact that Whimbrels also foraged at night at this site suggests that foraging time may have been limited by (possibly temperature related) activity rhythms of crabs over the low tide period.

Thus, although there was not a clear trend in daytime intake rates in relation to

tidal exposure time, the deviations from this trend could be explained in most cases by factors such as temporal variation in prey behaviour, rather than by invoking differences in the *intensity* of density-dependent effects. In view of the above patterns and considerations, there is a strong possibility that the numbers of Grey Plovers and Whimbrels at the sites in this study were limited by the availability of resources, in such a way that birds had to make maximal use of the time in which prey were available in order to meet their daily energy requirements.

The causes and consequences of a fixed *vs* versatile foraging method

Why do plovers have a stereotyped foraging method?

The ability of some intertidally foraging waders to forage tactilely lies in the abundance and distribution of sensory cells (Herbst corpuscles) in their bills (Bolze 1968 in Pienkowski 1981, Heppleston 1970) along with the evolution of long bills for probing. The short-billed plovers, however, are obligate visual foragers. The proportionally large eyes of plovers may serve to compensate for their lack of tactile ability, by providing greater acuity in detecting small prey both by day and night (Pienkowski 1983). My studies of Grey Plovers foraging at the Zwartkops estuary, where prawns on the surface were highly visible even to the human observer, led to an interesting observation. In most instances, it could be seen when a Grey Plover had sighted a prawn visible to the observer. When the sighted prawn was at some distance from the bird, the subsequent dash to the prey was always made in several bursts, and the stops along the way appeared to be in order to visually relocate the prey. The same behaviour was observed in Crab Plovers *Dromas ardeola* and Greater Sand Plovers *Charadrius leschenaultii* when running to capture large crabs at Mida Creek - although Crab Plovers are not true plovers, they use the same run-stop-search foraging technique. All three of these species frequently run towards prey with their head held sideways, using monocular vision. There is a possibility, therefore, that plovers are far less efficient or even unable to locate prey whilst they themselves are moving, necessitating their peculiar run-stop-search method of foraging.

Stereotyped foraging and versatile diets

The reason that Grey Plovers do not consume a larger proportion of the more energetically rewarding crustaceans in their diet is probably because they are less efficient than Whimbrels at catching certain types of crabs, due to their shorter bills and visual foraging method. Grey Plovers are unable to pursue crabs once they have retreated into their burrows. An extreme example was their difficulty in catching the abundant and highly visible, but swiftly retreating, fiddler crabs at Grande Rivière

Noire, which probably accounted for their low densities at this site. Other crabs, such as *Hymenosoma*, occur underwater or bury themselves under a layer of mud or in vegetation (pers. obs.), and, although remaining well within the reach of a Grey Plover, they have to be detected by tactile means. At the Berg estuary, the high density of cryptic *Hymenosoma* crabs was ignored, and polychaetes dominated the diet. A compounding influence was also the very high density of polychaetes at the Berg estuary (> 7000 *Ceratonereis* per m^2, Kaljeta & Hockey 1991). At the Zwartkops estuary, small surface-dwelling *Cleistostoma* crabs (which did not present the above problems), were abundant (monthly average maximum of 200 *C. edwardsii* $.m^{-2}$ (Feb), Els 1982), and prawns, though fewer were available, provided large energetic returns. At this site, very few polychaetes were consumed by Grey Plovers.

Thus it appears that Grey Plovers, because of their physical and behavioural limitations, are less adept at obtaining more profitable prey items than are Whimbrels, and are thus compelled to include a large proportion of small prey in their diet. Whimbrels, being flexible in their foraging behaviour, are better able to direct their foraging efforts at the more profitable prey species.

Does foraging behaviour constrain distribution in the nonbreeding season?

Plovers are considerably less numerous than sandpipers in cold north temperate areas (Prater 1981), whereas they make up a high proportion of shorebirds in more tropical localities. For example, at Mida Creek, Kenya, five plover species (*P. squatarola*, *Charadrius hiaticula*, *C. leschenaultii*, *C. mongolus* and including *D. ardeola*), and five sandpiper species (*N. phaeopus*, *Calidris ferruginea*, *C. minuta*, *Xenus cinereus* and *Tringa nebularia*) were common. Even where they make up a relatively large proportion of wader populations, however, plover numbers are unlikely to be comparable with those of sandpipers because of the spatial requirements of their obligate visual foraging method.

Pienkowski (1979) offered an explanation for the generally more tropical distribution of plovers than sandpipers in terms of the relative advantages of plover and sandpiper foraging 'strategies' in cold and warm conditions: because plovers cannot forage tactilely, they are at a disadvantage relative to sandpipers in cold conditions, when few prey are active at the surface. However, these generalisations do not explain why Grey Plovers are fairly common in cold north temperate areas and Whimbrels are uncommon north of Morocco (Smit & Piersma 1989).

The predominantly tropical nonbreeding distribution of Whimbrels has been linked to the abundance of large, surface active prey, particularly crustaceans (Chapter 1, Zwarts 1990). Their apparent dependence on large prey species is probably determined by their large body size relative to other sandpiper species. However,

Whimbrels do eat large polychaetes (Velásquez & Navarro 1993), and these (e.g. *Nereis diversicolor*) are relatively abundant in cold north temperate areas. Moreover, the Whimbrel's much larger relative, the Curlew *Numenius arquata*, is common in these latitudes (Smit & Piersma 1989), preying predominantly on these worms (Zwarts & Esselink 1989, Goss-Custard, Kay & Blindell 1977b), but reached by means of a bill almost twice as long as a Whimbrel's. Thus the high energy requirements of Whimbrels due to their large body size, coupled with their disadvantage relative to Curlews in reaching buried worms during low tide or cold spells, is probably the explanation for their virtual absence from these areas.

Large body size, on the other hand, may give the Grey Plover an advantage over most plovers in cold areas, due to the thermoregulatory advantage of a smaller surface-area to volume ratio (Bergmann's Rule), and this may explain their more extensive colonisation of the cold north temperate areas than most other plover species.

Foraging technique may provide sandpipers with an advantage over plovers in cold areas, but other factors such as body size and, for large sandpipers, bill-length, are probably also important in setting limits to species distributions.

CHAPTER 5

AGGRESSIVE BEHAVIOUR OF GREY PLOVERS AND WHIMBRELS IN TROPICAL AND SOUTH TEMPERATE WETLANDS

INTRODUCTION

Aggression amongst migrant waders during the nonbreeding season encompasses a variety of agonistic behaviour, ranging from mild threats, ground and air chases to protracted and ritualized territorial encounters and contact fighting. Although territorial encounters are almost always between conspecifics, other types of aggression also occur interspecifically, and nonterritorial aggression may involve disputes over items of food in addition to foraging space. Several studies have demonstrated a positive relationship between aggression rates and shorebird density (Recher & Recher 1969, Goss-Custard 1977b, Burger, Hahn & Chase 1979, Vines 1980, Metcalfe & Furness 1987) and a decrease in aggression rates at very high densities (Recher & Recher 1969, Puttick 1981, Stawarczyk 1984, Kalejta 1991). Differences in aggression rates between sites often cannot be ascribed to differences in bird density alone (Burger, Hahn & Chase 1979) and are probably further influenced by differences in the nature of the prey resources (Myers 1984). However, no studies have attempted to explain these differences empirically. Several facets of shorebird aggression need to be better understood before a reliable connection can be made between aggressive behaviour and competition.

In this study, Grey Plover and Whimbrel aggression was noted during observations of their foraging behaviour at a variety of sites in tropical and south temperate Africa and islands in the Indian Ocean. The following key questions were addressed:

1. What determines the nature and intensity of intraspecific aggression?;
2. What controls the rate of intra- and interspecific encounters over food?
3. What controls the rate of intraspecific encounters over foraging space?
4. How does aggression reflect intraspecific competition?

METHODS

Study areas

This study was carried out at nine sites in tropical and south temperate Africa and the Indian Ocean: Mida Creek, Kenya (03°22'S, 39°50'E); Mer Rouge (20°08'S, 57°30'E), Grande Rivière Noire (20°22'S, 57°22'E), Ile aux Benitiers (20°25'S, 57°21'E) and Passe de la Prairie (20°28'S, 57°20'E), Mauritius; and the Berg (32°47'S, 18°10'E), Zwartkops (two sites; 33°52'S, 25°38'E), and Breede River (34°24'S, 20°50'E) estuaries, South Africa. More detailed descriptions of the sites are given in Table 4.1 and Fig. 4.1 (Chapter 4). Studies were conducted at the same time of year as far as possible, all between February and April, except at the Breede estuary,

where observations were made in November.

Aggressive behaviour

Foraging behaviour was recorded during 1-minute (Whimbrels) and 10- to 15-minute (Grey Plovers) focal observations of birds selected at random. A minimum of 100 minutes, and usually more than 200 minutes, was obtained for each species at each site. All aggressive interactions that occurred during focal animal observations were recorded, and in addition, two to 17 hours of continuous observations were carried out at each site, during which all aggressive encounters observed in a prescribed area were recorded. For each interaction, the following were recorded:

a) duration, in seconds,

b) the aggressor and recipient species,

c) whether the encounter was over a food item, and

d) the nature of the interaction. Five categories were used:

1. threat (stationary posturing of one bird to another),
2. ground chase,
3. air chase (including chases which commence on the ground),
4. contact fight
5. territorial (ritualised parallel walking and posturing).

Foraging densities, behaviour and success

The numbers of Grey Plovers and Whimbrels were counted at half-hourly intervals on each study area, throughout at least two full low tide periods. Average densities were calculated for the period when the study area was at least 50% exposed.

During focal observations, several foraging parameters were recorded. The methods and results, including prey size and energy intake rates at the different sites, are described in detail in Chapter 4. Because Grey Plover foraging could be broken down into components, the following aspects of their foraging behaviour were used in the analysis of Grey Plover aggression: the number of steps taken per minute (step rate); and the number of steps per foraging move between search pauses or prey capture attempts (move length). In order to convert Grey Plover steps to distance travelled, pace lengths were measured from footprints at Mida Creek. Average pace length was 124.3 $\pm$ 34.6 (S.D.) mm (n = 331).

All incidents of raptors (Order Falconiformes) hunting in the vicinity of the study areas were recorded.

Table 5.1 The total number of aggressive encounters (enc) and aggression rates calculated at the different sites for Grey Plovers and Whimbrels from focal observations and from continuous observations. Average numbers of foraging birds used to calculated aggression rates from continuous observations are also given for each site.

	Focal observations			Continuous observations				
Site	*n* (min)	N (enc)	Enc/bird/h (E1)	*n* (h)	N (enc)	Mean n foraging	Enc/bird/h (E2)	E1/E2
A: GREY PLOVER								
Mida Creek	616	21	2.05	3.6	8	8.8	0.51	0.25
Mer Rouge*	104	9	5.19	10.0	29	14.5	0.40	0.08
Benitiers	193	5	1.55	16.8	22	13.6	0.19	0.12
Berg*	226	5	1.33	9.3	41	17.9	0.49	0.37
Zwartkops*	566	35	3.71	11.5	56	9.9	0.98	0.26
Z.Island	135	11	4.88	2.0	49	45.0	1.09	0.22
Breede	235	7	1.79	6.0	12	8.3	0.48	0.27
B: WHIMBREL								
Mida Creek	502	22	2.63	7.0	21	3.4	1.74	0.66
Mer Rouge*	240	11	2.75	10.0	55	16.0	0.69	0.25
G.R. Noire*	214	6	1.68	10.2	16	3.1	1.03	0.61
Benitiers	226	11	2.92	16.8	83	56.2	0.18	0.06
Prairie	205	7	2.05	7.4	12	13.3	0.24	0.18
Zwartkops	419	36	5.16	8.3	51	17.5	0.70	0.14

* Sites with fixed feeding territories

RESULTS

The rate of encounters recorded in continuous observations was consistently lower than in focal observations (probably due to simultaneous encounters being missed by the observer; E1/E2, Table 5.1). Thus the focal rates were used as the more accurate measure of encounter rate. However, encounters from both continuous and focal observations were pooled in calculating proportions of aggression types, and mean encounter duration.

Types of intraspecific aggression

The proportions of different types of intraspecific encounters varied between sites for both species and also differed for Grey Plovers and Whimbrels at the same sites (Fig. 5.1). Both territorial and nonterritorial aggression occurred at most sites.

Nonterritorial aggressive encounters were of short duration. Threat postures involved a fanned tail or raised wings and lasted only one to seven seconds. Ground chases were usually brief (Grey Plover: 3.3 ± 3.1 s, n = 30;

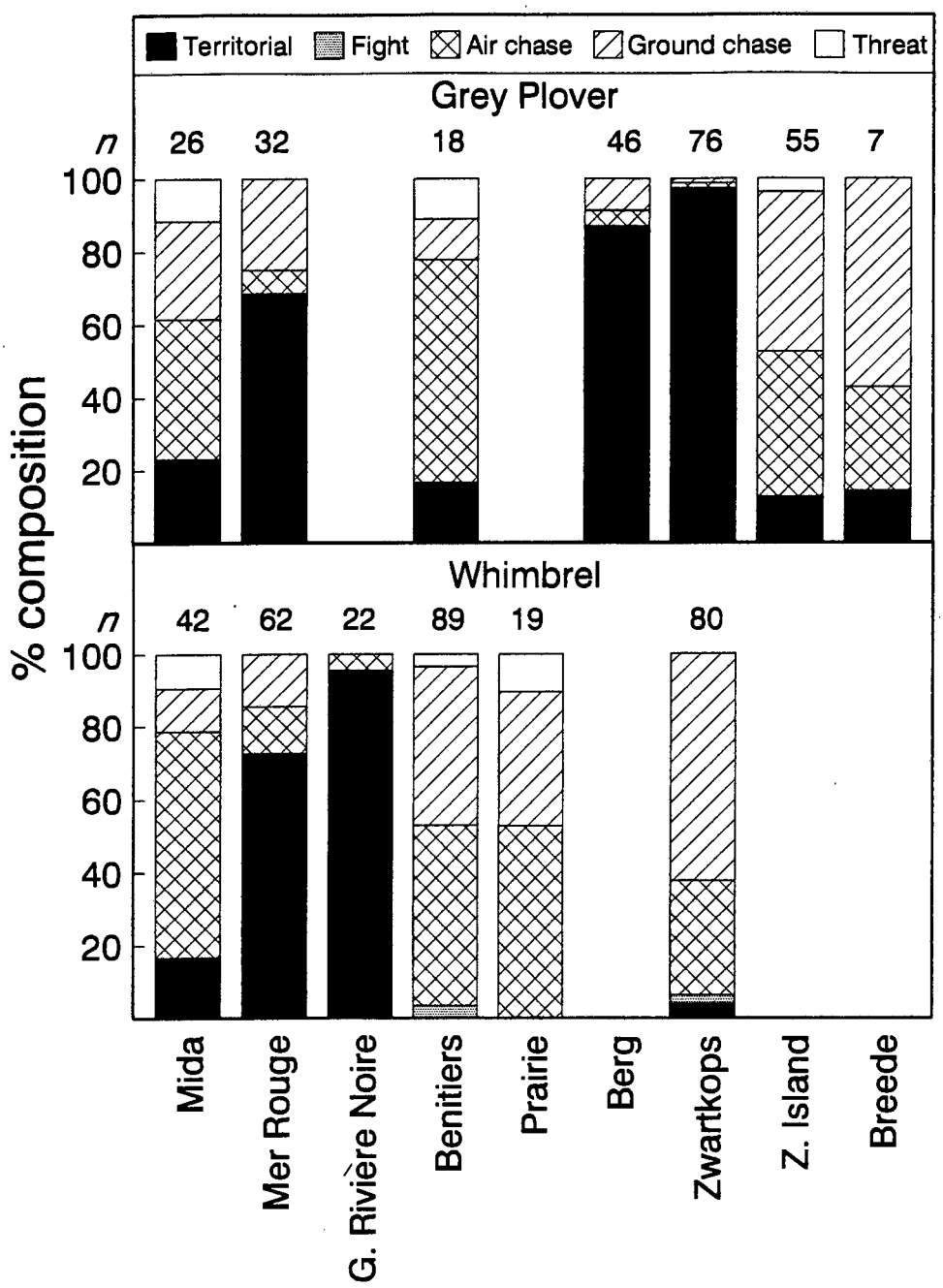


Figure 5.1. Relative frequency of different types of intraspecific aggression by Grey Plovers and Whimbrels at different sites.

Table 5.2. Duration of territorial encounters at sites where territories were fixed, and at nonterritorial sites.

Site	Grey Plover		Whimbrel	
	n	Duration (s)	*n*	Duration (s)
Fixed territory sites:				
Mer Rouge	15	157 ± 118	21	93 ± 64
G.R. Noire			9	117 ± 91
Berg	14	194 ± 227		
Zwartkops	57	181 ± 187		
Nonterritorial sites:				
Mida Creek	6	96 ± 79	6	53 ± 50
Benitiers	2	60, 900	0	
Prairie			0	
Zwartkops			2	20, 30
Zwartkops Island	7	28 ± 22		
Breede	1	27		

Whimbrel: 4.8 ± 4.4 (S.D.) s, $n = 72$), as were aerial chases (Grey Plover: 6.3 ± 9.3 s, $n = 32$; Whimbrel: 6.5 ± 12.7 s, $n = 65$), and both resulted in displacement of the recipient. The relative rate at which ground and aerial chases were carried out at different sites was related to the average density of conspecifics: a significantly greater proportion of air chases occured at sites with lower bird densities, both for Grey Plovers ($n = 7$, $r = -0.76$, $P < 0.05$) and for Whimbrels ($n = 6$, $r = -0.88$, $P < 0.05$; Fig. 5.2).

Fixed feeding territories were defended by Grey Plovers at Mer Rouge and the Berg and Zwartkops estuaries, and by Whimbrels at Mer Rouge and Grande Rivière Noire: ritualized territorial aggression was the dominant form of interaction in these cases (Fig. 5.1). At Mer Rouge, territories of Whimbrels and Grey Plovers overlapped interspecifically, and adjoined an area where birds of both species gathered to roost. Non-ritualized interactions by both species at this site were directed at birds which strayed from this roosting group. Similarly, nonterritorial-type encounters by territorial Grey Plovers at the Berg and Zwartkops estuaries were with outside intruders rather than neighbouring territory holders. Territorial-type ritualized encounters were occasionally recorded at sites where fixed territories were not defended.

Territorial encounters among both Grey Plovers and Whimbrels were highly variable in duration, ranging from a few seconds to 15 minutes. The average duration of territorial encounters did not vary significantly between the sites where fixed territories were held (Table 5.2; Grey Plovers: $ANOVA_{2,83}$, F-ratio = 0.156, n.s; Whimbrels: Student's t-test, $t = -0.89$, n.s). However, ritualized interactions at these sites were significantly longer than at sites without fixed territories for Whimbrels ($t = 2.046$, $P < 0.05$), and for Grey Plovers, with the exception of interactions at Ile aux Benitiers, ($t = 2.46$, $P < 0.05$). Territorial interactions between Grey Plovers at Ile

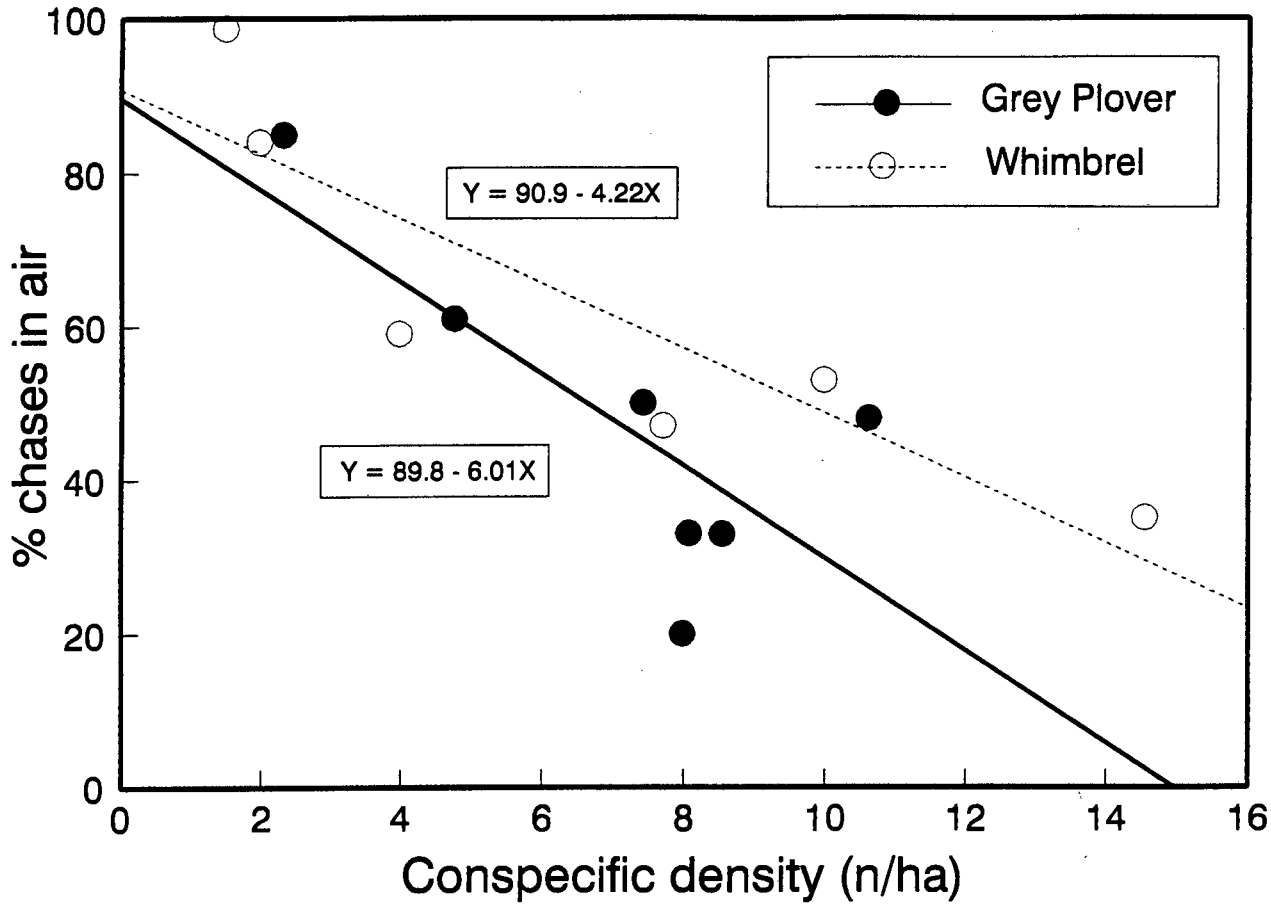


Figure 5.2. Relationships between the percentage of intraspecific chases which were aerial and conspecific density of Grey Plovers and Whimbrels at different sites.

Table 5.3 The percentage of aggressive encounters at each site which were interspecific, and the percentage of all intra- and inter-specific encounters which were directly over food (i.e. potential or realized kleptoparasitism).

	GREY PLOVER			WHIMBREL		
	% inter-	% kleptoparasitic		% inter-	% kleptoparasitic	
Site	specific	intraspecific	interspecific	specific	intraspecific	interspecific
Mida Creek	10	0	66	2	0	0
Mer Rouge	13	0	80	6	0	75
Grande Rivière Noire	-			0	0	-
Ile aux Benitiers	36	6	90	5	7	20
Passe de la Prairie	-			0	0	-
Berg	0	2	-	-		
Zwartkops	16	0	73	8	3	4
Zwartkops Island	8	15	40	-		
Breede	0	14	-	-		

aux Benitiers were all between two individuals at the end of a muddy peninsula, and lasted up to 15 minutes.

Territorial defence was not related to size or type of prey at different sites. Fixed territories were defended at sites with the largest prey (Zwartkops estuary - Grey Plovers) and the smallest (Berg estuary - Grey Plovers; Chapter 4), and at sites where energy intake rates were high (Grande Rivière Noire - Whimbrels), intermediate (Zwartkops - Grey Plovers) and low (Mer Rouge - both species; Chapter 4). In addition, territories were defended at sites where birds occurred at high densities (Mer Rouge - both species, Berg and Zwartkops estuaries - Grey Plovers) and low density (Grande Rivière Noire - Whimbrels; Chapter 4).

Both territorial and nonterritorial populations occurred at sites where avian predators were absent (Mauritius), rare (Zwartkops - less than 1 disturbance per month - Lanner Falcon *Falco biarmicus*, African Fish Eagle *Haliaeetus vocifer*) and occasional (Berg - less than 1 disturbance per day - Peregrine Falcon, *F. peregrinus*, Lanner Falcon, Booted Eagle *Hieraaetus pennatus*, African Fish Eagle, African Marsh Harrier *Circus ranivorus*, Black Harrier *C. maurus*), but fixed territories were not defended at Mida Creek, where raptors were common (average 6 ± 3 (S.D.) disturbances per daytime low tide period (n = 7) - Peregrine Falcon, African Fish Eagle, Montagu's Harrier *C. pygargus*).

Intra- and interspecific aggression over food

Interspecific encounters formed a small proportion of the aggressive encounters recorded for both species, particularly Whimbrels (Table 5.3). Attempted and successful kleptoparasitism (food stealing) occured both intra- and interspecifically, but was more prevalent in interspecific encounters (Table 5.3).

Table 5.4. The species involved in interspecific interactions with Grey Plovers and Whimbrels for space and for food.

	For Space:		For Food:	
Site	aggressor	victim	aggressor	victim
GREY PLOVER:				
Mida Creek		*Dromas ardeola*	*D. ardeola*	*Calidris alba*
Mer Rouge		*Arenaria interpres*	*N. phaeopus*	*N. phaeopus* *Sterna hirundo* *Charadrius leschenaultii*
Benitiers	*N. phaeopus*	*C. leschenaultii*	*N. phaeopus* *	*A. interpres* (9)
Zwartkops	*N. phaeopus*	*N. phaeopus* *Tringa nebularia* *C. leschenaulti* *C. marginatus*	*Larus dominicanus* (9)	*A. interpres* *N. phaeopus*
Z. Island	*S. hirundo* (2)	*S. hirundo*	*L. dominicanus*	*S. hirundo*
WHIMBREL:				
Mida Creek	*D. ardeola*			
Mer Rouge		*C. leschenaultii*	*P. squatarola*	*P. squatarola* * *S. hirundo* *C. leschenaultii*
Benitiers		*P. squatarola* (2) *A. interpres* *T. nebularia*		*P. squatarola*
Zwartkops	*P. squatarola*	*S. hirundo* *P. squatarola* * *T. nebularia*	*L. dominicanus* *P. squatarola*	*A. interpres* *S. hirundo*

* incidental records outside observation times

Intraspecific kleptoparasitism did not occur at sites where birds defended fixed foraging territories, except in one instance at the Berg estuary, which involved the theft of an unusually large polychaete worm by a juvenile from an adult Grey Plover.

The aggressor was the larger species in 87% of the interspecific encounters recorded during focal and continuous observations (Table 5.4). At Ile aux Benitiers, Grey Plovers actively followed foraging Turnstones *Arenaria interpres* until the latter uncovered hidden crabs. At the Zwartkops estuary, Grey Plovers were frequently harassed by Kelp Gulls which stole 6% (5/86) of their prawn catch. At the Zwartkops and Breede estuaries, where birds consumed large *Upogebia* as well as smaller prey

species, all intra- and interspecific kleptoparasitic encounters involved these mudprawns.

The rate of kleptoparasitic encounters initiated by both Grey Plovers and Whimbrels, and directed both intra- and interspecifically, was related to energy intake rate (Fig 5.3): kleptoparasitic encounter rates of Grey Plovers (at all sites other than the Breede estuary), and for Whimbrels, with the exception of the Zwartkops estuary, were significantly inversely related to energy intake rates ($n = 6$, $r = -0.93$, $P < 0.01$ and $n = 5$, $r = -0.94$, $P < 0.05$, respectively).

Intraspecific aggression over space

Grey Plover intraspecific aggression rates (excluding encounters over food items) were positively, but not significantly, related to average bird density ($n = 7$, $r = 0.71$, $P = 0.07$; Fig. 5.4a). This relationship was significant for Whimbrels, however ($n = 6$, $r = 0.88$, $P < 0.05$; Fig. 5.4b).

In order to test whether the nature of the prey resources plays a role in determining aggression rates of Grey Plovers, a model was developed incorporating search area and walking speed as well as bird density, based on the findings that Grey Plover search radius (indicated by average move length) and walking speed are influenced by the prey base (Chapter 4). Hypothetically, circles of diameter d (representing a bird's search area) at a certain density D and moving randomly in relation to one another at an average velocity v (walking speed) will have a mean free path (average distance between successive collisions) as follows:

$$\text{mean free path} = 1/(\sqrt{2}.d.\text{D}),$$

and "collision rate" is determined by the velocity as:

$$\text{collision rate} = v/\text{mean free path} = v/(\sqrt{2}.d.\text{D})^{-1}.$$

Thus the collision rate can be doubled by doubling either the search diameter (d), bird density (D) or travel velocity (v; Fig. 5.5).

In the case of Grey Plovers, the search area diameter was taken to be equivalent to the average length of foraging moves between searching for prey, and the velocity as the distance moved per unit time. Expected 'collision' rate explained aggression rates of Grey Plovers better ($r = 0.85$, $P < 0.02$; Fig. 5.6) than did bird density alone ($r = 0.71$, n.s., Fig. 5.4a).

Theoretically, the slope of this relationship should be unity, assuming the direction of movement of all individuals to be random. However, the direction of movement is strongly non-random between birds (Chapter 2), probably accounting for the low slope of 0.17.

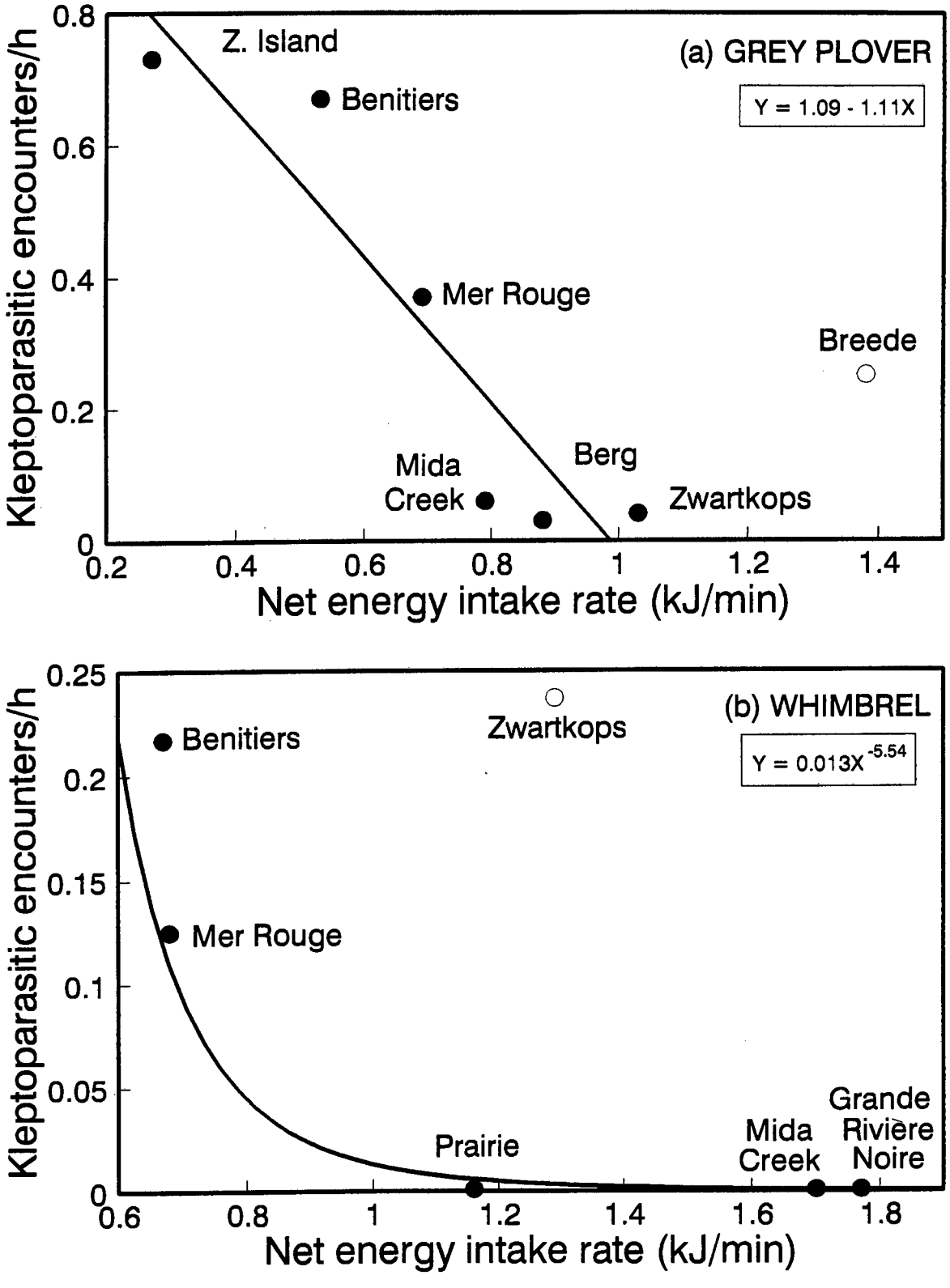


Figure 5.3. The relationship between the rate of intra- and interspecific kleptoparasitism initiated by (a) Grey Plovers and (b) Whimbrels and their net energy intake rates at the different sites. Open circles are not included in the regression.

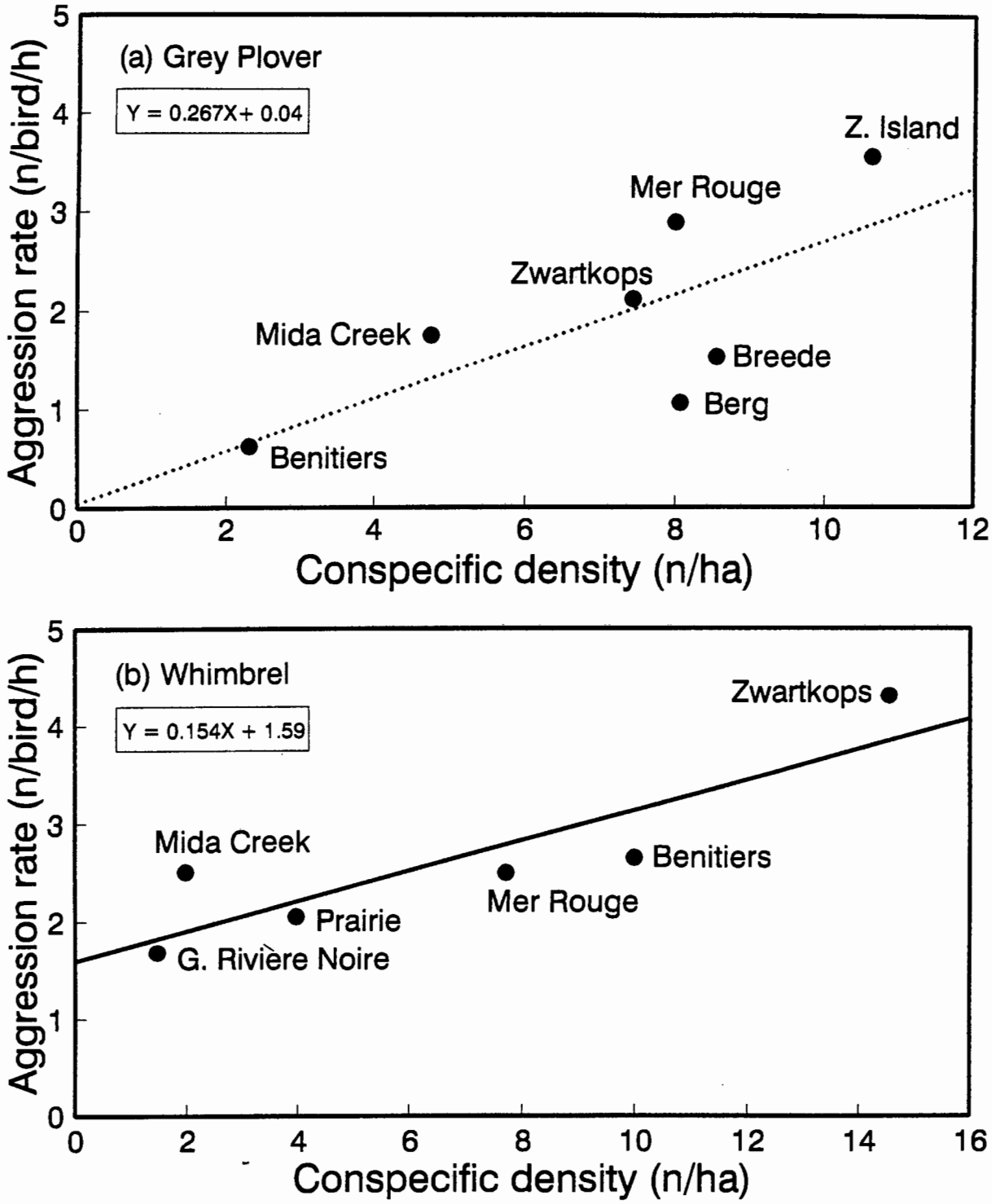


Figure 5.4. Relationships between the rates of intraspecific, nonkleptoparasitic encounters and conspecific density of (a) Grey Plovers and (b) Whimbrels at the different sites.

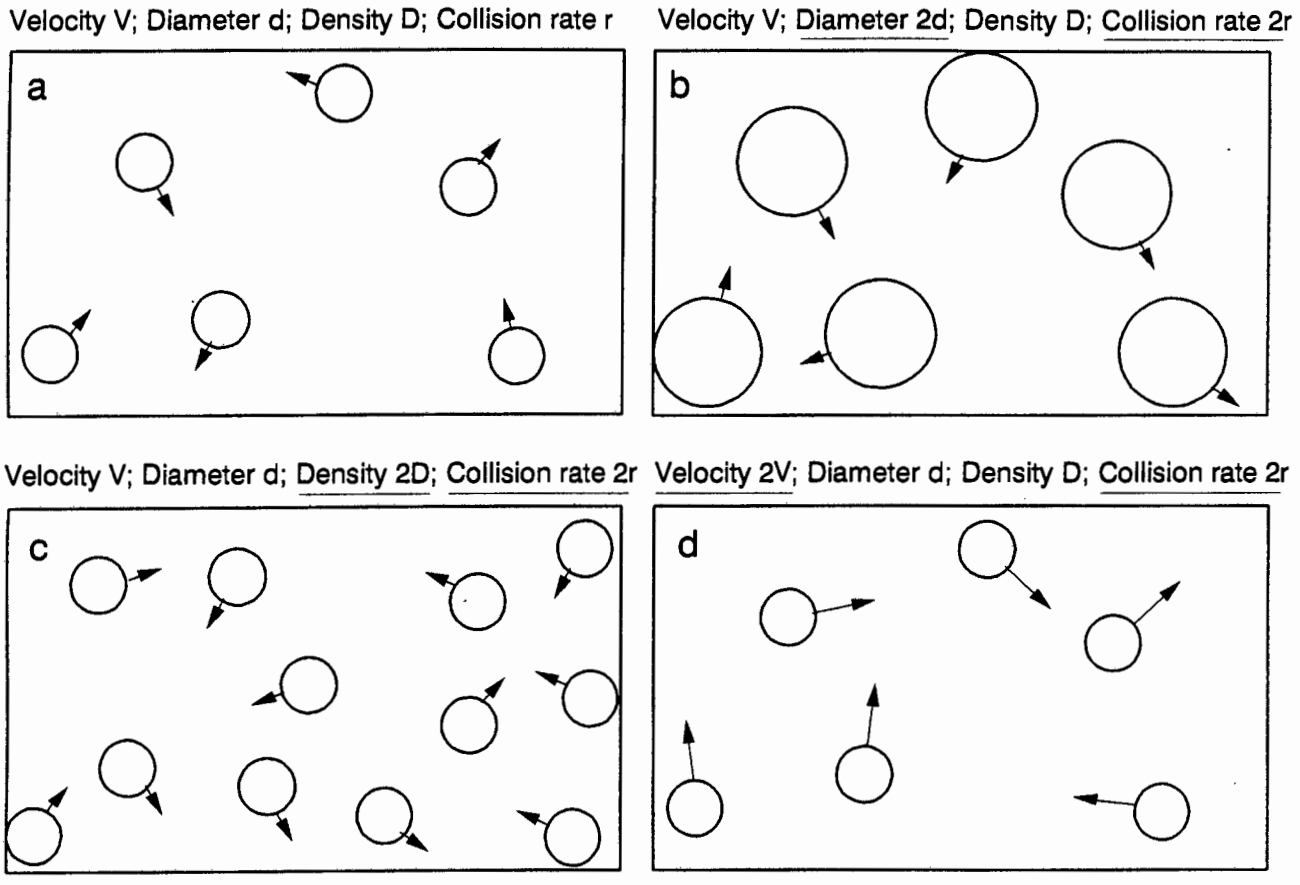


Figure 5.5. Diagram illustrating the influence of circle velocity, diameter and density on their collision rate. The circles represent the search area of a foraging bird.

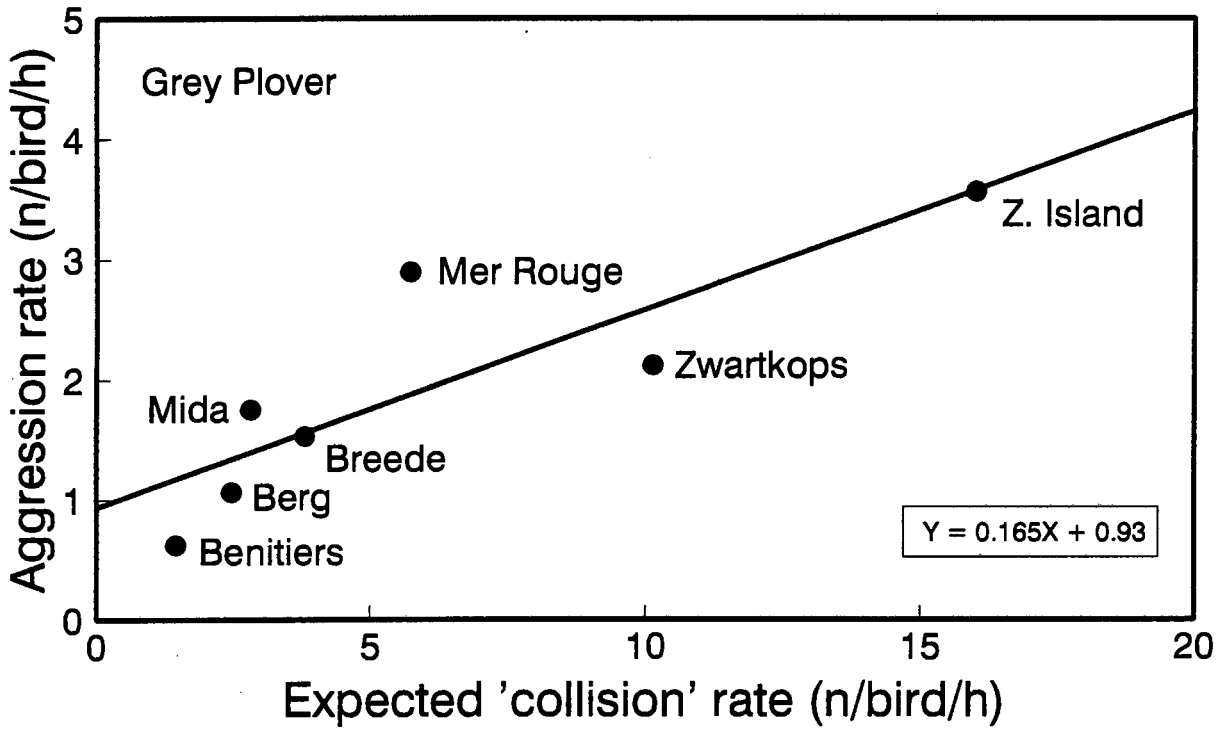


Figure 5.6. Relationship between the frequency of non-kleptoparasitic intraspecific aggression and the expected 'collision' rate as a function of conspecific density (n/m^2), search area radius (m) and walking speed (m/h) at each site.

DISCUSSION

Determinants of aggression type

A major behavioural dichotomy observed in this study was the defence of fixed territories by the majority of Grey Plovers or Whimbrels at some wetlands and not at others. Much research has been devoted to explaining the spacing behaviour of foraging birds (e.g. Goss-Custard 1970, 1976, 1985). Cohesive flocking may be beneficial to birds, despite the trade-off of increased aggression and interference, in that (a) the chances of finding patches of food may be increased (Clark & Mangel 1984), (b) vigilance effort per individual is reduced (Abramson 1979, Fleischer 1983), and (c) the probability of being singled out by a predator is decreased (Myers 1980, Buchanan *et al.* 1988). The latter is supported by the fact that flocking is rare on some islands which lack avian predators (Lack & Lack 1972, Willis 1972), and is thought to be a particulary strong driving force for flocking among waders (Goss-Custard 1985). The assumption implicit in the above is that territoriality, which involves an 'overdispersed' distribution (*sensu* Stinson 1980), will be inhibited when the risk of predation is high.

However, the above benefits apply more to tactile than to visual foragers. Firstly, visual foraging methods require more space per individual per unit time than do tactile foraging methods. Visual foragers are more prone to interference by neighbours (Goss-Custard 1976) and consequently, are more aggressive than tactile foragers in defence of personal space (Burger *et al.* 1979). Increased densities of visual foragers thus reduce, rather than enhance, prey capture rates (Goss-Custard 1976). As a result, visual foragers in general, and Grey Plovers in particular (Stinson 1977), are overdispersed when foraging, whether territorial or not. In addition, Whimbrels only foraged in close proximity when foraging tactiley (Chapter 4). Secondly, visually foraging birds are automatically more vigilant, because they search for prey in an upright stance. Although Grey Plover and Whimbrel vigilance in this study was frequently observed at Mida Creek, where raptors occurred more frequently than at other sites, this involved negligible interruption of foraging activity. Thirdly, the risk of being singled out by a predator can be reduced by a temporary change in behaviour. Territorial birds in this study usually abandoned their territories and coalesced into flocks for a short period in the event of any disturbance, as has been found for territorial Buff-breasted Sandpipers *Tryngites subruficollis* (Myers 1980), African Black Oystercatchers *Haematopus moquinii* (Hockey 1985) and Redshanks *Tringa totanus* (Whitfield 1988). However, at Mida Creek, larger species, including Grey Plovers, occasionally crouched instead of taking flight in response to raptors.

Territoriality is thus more likely to occur amongst visually than tactilely

foraging birds.

Although Grey Plovers and Whimbrels at Mida Creek were evenly spaced over the intertidal area, frequent disturbance by predators could have discouraged territorial behaviour at this site for the reason that they would have to spend too much time renegotiating boundaries at each subsequent landing (Myers 1980). On Mauritius, there are no raptors which hunt shorebirds, yet Grey Plovers and Whimbrels defended fixed territories at some sites but not others. Thus predation risk, if it has any influence on the spacing behaviour of visual foragers at all, is not necessarily an overriding factor in determining whether fixed territories are defended.

Several factors are purported to promote territory defence, including the patchiness and scarcity of prey (Recher & Recher 1969, Sullivan 1986). Although the former was not evident at the sites in this study, energy intake rates and kleptoparasitism rates at Mer Rouge and Ile aux Benitiers suggested that prey were scarce at these sites. Territories, however, were only defended at the former.

In this study, the incidence of territoriality was not related to energy intake rate, prey size or bird density. However, territory defence by Whimbrels at Grande Rivière Noire may have been influenced by the behaviour of their prey. Whimbrels at this site foraged on fiddler crabs *Uca marionis* which reacted to the presence of foraging birds by rapidly retreating down their burrows, thus creating a large, crabless halo around each forager. This neccessitated long rapid dashes by Whimbrels in order to capture their prey, a situation more prone to interference by neighbours than the normal steady, walking search used by this species. The birds at Grande Rivière Noire have a large search radius (prey are highly visible) and a high travel velocity, both conditions which increase the 'collision rate' (Fig. 5.5).

Seasonal studies at the Zwartkops estuary indicate that territorial defence is influenced by intraspecific competition (Chapters 1 and 2), and certain behavioural changes were associated with increasing levels of competition during the residence period. Grey Plovers and Whimbrels at the Zwartkops estuary did not defend territories during the austral winter, when the number of birds was low, energy intake rates were high, and competition was minimal, but both species commenced territorial defence in spring, after a threshold density of conspecifics was reached with the arrival of migrants. Grey Plovers defended fixed territories for the rest of the austral summer, but Whimbrels, which defended larger territories, ceased territorial defence by early summer, as their numbers on the estuary continued to increase. Whimbrels at the Zwartkops estuary forage at the highest densities recorded in the Afrotropics, and territoriality was probably abandoned due to their density being too high for defence to be worthwhile, a situation of intense interference competition. Thus territory defence is probably only viable at intermediate levels of prey availabilty per bird, which is

influenced not only by the abundance, but by the type, and particularly, behaviour, of prey.

Territorial encounters, involving ritualised parallel walking or running, also occurred at sites where fixed territories were not defended. These probably represented occasional, unsuccessful attempts by individuals to establish territories. Similarly, nonterritorial type encounters occurred at sites where fixed territories were defended, but in these instances aggression by territorial birds was directed at nonterritorial intruders. These encounters differed in nature from those directed at neighbouring territory holders, but were territorial in function.

The majority of aggression at sites without fixed territories occurred in the form of chases. Whether the chases took place on the ground or in flight was related to the density of foraging birds. Whereas ground chases would be energetically more economical over short distances, there will be some threshold distance beyond which it is more efficient to fly. The more passive threat interactions were less common, and probably served to warn the recipient before the latter had encroached into the aggressor's foraging space. It is possible that some forms of threat are so subtle as to remain undetected by human observers.

Interspecific aggression occurred much less frequently than intraspecific aggression. This is usually the case amongst mixed species foraging assemblages of shorebirds (e.g. Recher & Recher 1969, Burger *et al.* 1979, Kalejta 1991). Stinson (1977), however, reported a higher proportion of inter- than intraspecific aggression by nonbreeding Grey Plovers in the United States, which he ascribed to intraspecific mutual avoidance behaviour, and as a result, higher inter- than intraspecific competition (Stinson 1980), and further suggested that these proportions should be reversed only when foraging space was limited. However, avoidance behaviour is a manifestation of competition, in that it implies constraints on the immediate choice of foraging site. In Stinson's study, Grey Plovers foraged in non-random association with other species, most of which were smaller than Grey Plovers. Thus it is possible that Grey Plovers were foraging in association with these birds in order to kleptoparasitize them, as was seen commonly at Ile aux Benitiers.

Determinants of kleptoparasitism rates

The incidence of kleptoparasitic encounters appeared to be influenced by two factors - the energy intake rates of the birds, and the presence of very large prey. The former relationship suggests that birds resort to kleptoparasitic attacks when their own foraging success is low. In Kelp Gulls *Larus dominicanus*, kleptoparasitism is most prevalent among those age classes that have the greatest difficulty in satisfying their energy demands through 'hunting' alone (although all prey were essentially the same size;

Hockey & Steele 1989), supporting the idea that kleptoparasitism can arise through energy limitation.

Increased incidence of kleptoparasitism when prey are large, such as for mudprawns at the Zwartkops estuary, has been shown experimentally for Kelp Gulls (Hockey & Steele 1989). Not only is the relative return for the effort of stealing higher for large prey, but the longer handling times for larger prey (Chapter 1) afford a greater chance of success to the parasite.

Kleptoparasitism in flock foraging species has also been found to increase with increasing flock density (Metcalfe & Furness 1987), and this factor may have played a role in the high intraspecific kleptoparasitism rates amongst Grey Plovers at Zwartkops Island and Whimbrels at Ile aux Benitiers (Table 5.1).

Intraspecific encounters over foraging space

Differences in aggression rates between sites cannot always be explained by differences in bird density (Burger *et al.* 1979, this study), and it has been suggested that unexplained differences could be related to differences in prey characteristics, such as availability, abundance or size (Myers 1984). The drawbacks in attempting to measure factors such as prey availability from the birds' perspective are well known, and it may therefore be difficult to link such parameters to aggression. However, aspects of foraging behaviour do change from site to site, in response to differences in the nature of prey resources (Chapter 4), and provide a useful 'summation' of these factors. Although the search radius of a Grey Plover may not be exactly equal to its average move length, is it likely to be proportional to this distance, and move length, which varies between sites in relation to the type of prey captured (Chapter 4) is the only available index of search area. In this study, aggression rates (other than kleptoparasitic aggression) were related both to foraging density and a combination of foraging density, search area and walking speed. Thus aggressive encounters over space, although differing in nature and duration, occur in response to the balance between individuals' foraging space requirements (dictated by the type of prey) and the density of birds. Although both territorial and nonterritorial visually foraging birds usually move in such a way as to reduce the frequency of encounters (Chapter 2, Stinson 1977), it is to be expected that encounter rates will be proportional if not equal to the frequency predicted if their movements were random, as demonstrated here for Grey Plovers.

Aggression rates vary seasonally due to social factors as well as competition. The aggression rates of territorial Grey Plovers at the Zwartkops estuary decreased throughout the residence period, despite increasing pressure on prey resources and reduced energy intake rates, and this was ascribed to increased neighbour familiarity

(Chapter 2). Under similar conditions, after an initial peak during the spring arrival period ascribed to social factors and territory establishment (Chapter 1), Whimbrel aggression rates remained fairly constant throughout the austral summer, and this was probably also due to increasing familiarity amongst foraging birds. During this study, aggression rates compared were all recorded between February and April, with the exception of the Breede estuary (November), in order to keep the 'familiarity factor' as constant as possible. Nevertheless, other factors influencing seasonal aggression rates may differ between sites, and one can only derive limited conclusions from short-term studies.

Aggression, competition and limited resources

An understanding of the links between aggressive behaviour, resource limitation and competition is essential in order to make intersite comparisons of foraging conditions. Competition, as it affects an individual, is defined here as occurring when a food resource, or a factor affecting access to food resources (e.g. space), is limited by the presence of other individuals.

Where food is spatially scarce, a low intake rate can occur when the spatial requirements for foraging exceed the capabilities of an individual, and individuals may then struggle to obtain their daily energy requirements in the absence of competition: a lack of evidence for competition does not automatically mean that resources are not limiting. Nevertheless, the fact that individuals occupy habitats where food resources are scarce implies that they may be forced to do so because of competition for sites where food is abundant. This situation was illustrated by Grey Plovers at Ile aux Benitiers, where conspecific densities and aggression rates were low. The scarcity of food available to Grey Plovers at this site was reflected in a combination of low bird density and low energy intake rates, and also in the way in which they exploited (through kleptoparasitism) the ability of Turnstones to find food; Turnstones themselves were probably an important resource at this site.

The kleptoparasitic response to large prey caught by other birds can be opportunistic, and can occur independently of resource limitation. Attempted kleptoparasitism may also occur because of resource limitation, which in turn may be caused by competition, or by absolute scarcity of resources, such as in the above case. Regardless of the motivation for kleptoparasitism, this behaviour will be limited by the frequency of opportunities for its occurrence, which will depend partly on the size of prey involved, and partly on the availability of potential hosts. Kleptoparasitism is thus an unreliable indicator of competition, but may strengthen evidence of resource limitation in situations where energy intake rates are low.

Aggressive encounters over space are associated with direct competition for

access to food resources (interference competition) and the frequency with which they occur is likely to be influenced by the specific spatial requirements for foraging at a particular site. Visual foragers require more instantaneous foraging space than tactile foragers; this is especially true of plovers with their stereotyped 'run-stop-search' foraging behaviour. In addition, there may be a trade-off between benefits obtained by mutual avoidance of competitors, which reduces the frequency of direct interaction, and the costs of deviating from a preferred foraging route. The behavioural response of an individual will be that which minimises the negative effects of interference competition at the lowest net cost. I suggest that an increase in the level of potential interference from conspecifics leads to a gradation in the behaviour of visual foragers from mutual avoidance, to overt aggression and then territoriality. Further increases in interference competition will lead to abandonment of territories and resumption of overt aggression. However, the levels of competition which induce these changes in behaviour will be site- as well as species-specific.

The relationship between the rate of aggression over foraging space and the spatial requirements of birds and foraging density indicates that aggression rates provide a reliable indication of the level of interference competition, despite the fact that the duration and nature of aggressive encounters vary considerably. However, based on the findings in Chapter 4, the level of interference competition cannot be used as an indication of the overall effects of competition, or the foraging performance of birds at different sites.

In conclusion, competition for resources is reflected in a complex combination of aspects of the foraging ecology and distribution of individuals, only one aspect of which is the overt expression of the proximate level of interference. Broad-scale inferences about relative competition levels and the degree to which resources are limited cannot be made on the basis of social behaviour alone.

CONCLUSIONS AND SYNTHESIS

CHAPTER 6

PERSPECTIVES ON THE EVOLUTION OF VARIABLE MIGRATION DISTANCE IN GREY PLOVERS AND WHIMBRELS

SUMMARY

1. Ecological correlates of migration distance were investigated for Grey Plovers and Whimbrels in the Palaeo-Afrotropical regions of their nonbreeding ranges.

2. Numbers of both species are greatest in the north of their ranges, but bird densities tend to be highest at wetlands in the south. Birds spend the shortest amount of time on the most southerly nonbreeding sites.

3. There was no evidence of any clinal change in size related to latitude for either species, based on wing lengths. Female Grey Plovers migrate further south than males, based on sex ratios of museum specimens. Whimbrels are sexually dimorphic, but the distribution of bill lengths in the south of their range did not suggest any sexual difference in migration distance.

4. Seasonal patterns of weight gain and loss differed markedly between north temperate and south temperate sites, reflecting differences in environmental conditions and departure times. Birds in the tropics were generally of lower body mass, and may not fatten to the same degree as birds at temperate sites prior to migration. Midwinter weight loss in the north temperate zone suggests that the risk of starvation is highest in the north.

5. Seasonal patterns of energy intake rates vary from north to south, and energy intake rates generally are highest in the south. In addition, decreased thermoregulatory costs and increased photoperiod confer energetic advantages on birds spending the nonbreeding season further south.

6. Risk of predation was lowest at the southernmost sites.

7. Intrasexual variation in migration distance, evidence for increased within-'winter' survival towards the south and evidence against decreased competition towards the south are discussed in terms of current hypotheses for the mode of evolution of migration patterns.

INTRODUCTION

Avian migration patterns are complex and diverse, forming a continuum from partial migration to complete, long-distance migration. Many shorebird species fall at the latter end of this continuum, breeding at high northern latitudes and migrating south to occupy a broad range of latitudes during the nonbreeding season. Grey Plovers and Whimbrels both breed in the Palearctic and Nearctic regions; Grey Plovers at polar latitudes, and Whimbrels slightly farther south in north temperate and polar latitudes. During the nonbreeding season, both species occur on the coasts of all the continental landmasses except Antarctica, spanning over 100° from north to south temperate latitudes (Hayman, Marchant & Prater 1986).

A certain degree of structure has been identified in shorebird migration patterns (e.g. leap-frog migration - Swarth 1920, Alerstam & Hogstedt 1980, Boland 1990, intersexual differences in migration distance - Myers 1981), but the problem of interpreting these patterns in an evolutionary perspective remains 'a very thorny one' (Drent & Piersma 1990). Within these patterns, the variation in migration distance between birds of a certain group (e.g. a northerly breeding population, or a particular sex) is often considerable, and this is one of the aspects of migration that has not been adequately explained.

Hypotheses concerning the evolution of migration patterns are traditionally competition-based (e.g. Cox 1968, Von Haartman 1968), but physiological and demographic hypotheses have been offered as alternatives (e.g. Ketterson & Nolan 1979, Greenberg 1980). Tests of these hypotheses have been limited by a lack of empirical evidence, both of the importance of competition and of the survivorship of birds employing different migratory options (Cox 1985, Fretwell 1980, Hockey *et al.* 1992). Most evidence that has been presented to date is from a limited range of latitudes, or from different altitudes (e.g. Greenberg 1980, Ketterson & Nolan 1982, 1983, Pienkowski & Evans 1985), and the importance of obtaining comparative data from a broader range of latitudes has been highlighted (Castro, Myers & Ricklefs 1992).

In this study, the foraging ecology of Grey Plovers and Whimbrels was examined at several tropical and south temperate sites. Factors which influence the behaviour and energetics of these species were examined from a seasonal perspective (Chapters 1 and 2), a diel perspective (Chapter 3) and from the perspective of inter-site variation in foraging conditions (Chapters 4 and 5). This chapter draws upon the above studies and information from the literature in order to investigate the relative consequences of migrating to different latitudes. The data used are limited mainly to the eastern Atlantic and western Indian Ocean parts of the nonbreeding range. As an

essential background, latitudinal patterns in the distribution and morphology of Grey Plovers and Whimbrels are presented in the following section. Although this study does not provide survivorship data, evidence is sought for factors that may influence within-'winter' survival. The findings are interpreted in terms of current thinking on the evolution of migration patterns, and the implications for conservation are discussed.

LATITUDINAL PATTERNS IN DISTRIBUTION AND MORPHOMETRICS

Numbers and densities

Within the western Palearctic and Afrotropical parts of their nonbreeding range, the greatest numbers of both species are found in the north, and only a small percentage migrate as far as the southern tip of Africa (Fig. 6.1; Appendix 6.1). This pattern is particularly clear on the east Atlantic seaboard, and can be explained largely by a much greater availability of suitable habitats in the north than in the south. Shorebird counts have not been undertaken throughout a large area from the Gulf of Guinea to Angola, and in Mozambique.

Hockey *et al.* (1992) demonstrated that shorebird densities increase logarithmically towards the south at 31 wetlands along the East Atlantic flyway. The same analyses were performed in this study for Grey Plovers and Whimbrels at a total of 50 wetlands along the east Atlantic and western Indian Ocean coasts, for comparison. Although absolute numbers are greatest in the north, Grey Plover and Whimbrel densities tend to be highest in the more southerly wetlands (Fig. 6.2; Appendix 6.2). The trend was significant for Grey Plovers ($n = 50$, $r = 0.63$, $P < 0.001$; latitude linearised positively from 60°N = 1, 59°N = 2, etc.), but not for Whimbrels ($n = 22$, $r = 0.32$, n.s.). Wetlands exceeding 10 000 ha are common in northern parts of the east Atlantic flyway, but most coastal wetlands in southern Africa have an intertidal area of less than 2 000 ha. Grey Plover densities were negatively correlated with wetland area ($r = -0.63$, $P < 0.001$), and both latitude and wetland area significantly influence Grey Plover densities when the other independent variable is held constant by partial correlation analysis (latitude (L): $r = 0.37$, $P < 0.05$; wetland area (A, ha): $r = -0.43$, $P < 0.01$). The relationship between Grey Plover density (D) and both these variables is described by the equation: $\log D = 0.14 + 0.008L - 0.026 \log A$ ($F = 21.1$, df = 2,47, $r = 0.69$, $P < 0.001$). Eight percent of the variance was explained by latitude, and 39% was explained by wetland area. This differs considerably from the pattern of 40% and 10% explained by latitude and area respectively for all shorebirds (Hockey *et al.* 1992). However, Grey Plover density was still significantly correlated with latitude when only small wetlands ($\leq$ 3 000 ha) were used in the analysis ($n = 31$, $r = 0.50$, $P < 0.01$).

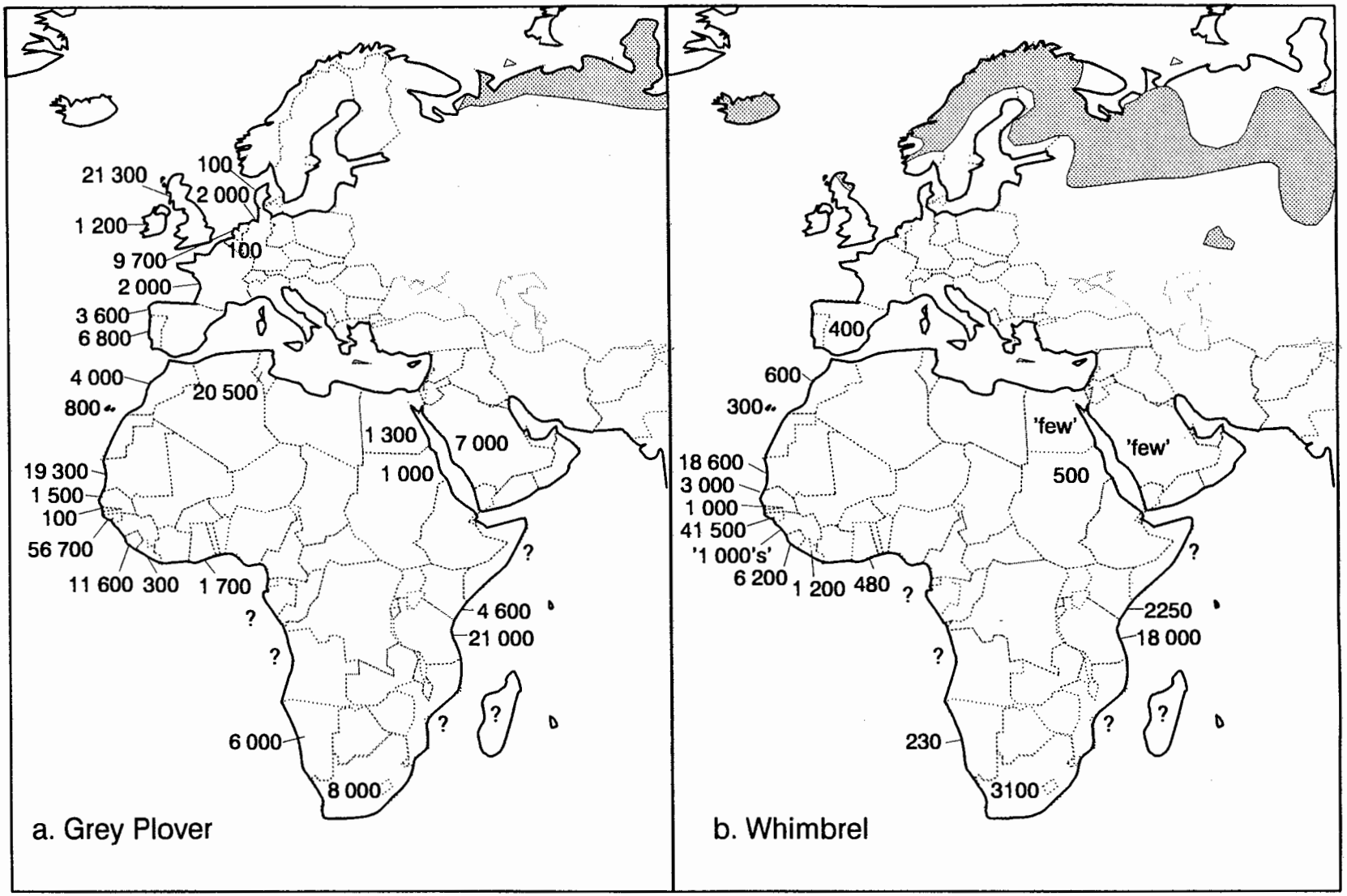


Figure 6.1. Numbers of Grey Plovers and Whimbrels in coastal countries of the east Atlantic and western Indian Ocean (countries and sources listed in Appendix 6.1). The western Palearctic parts of their breeding ranges are shown in grey (from Cramp & Simmons 1983).

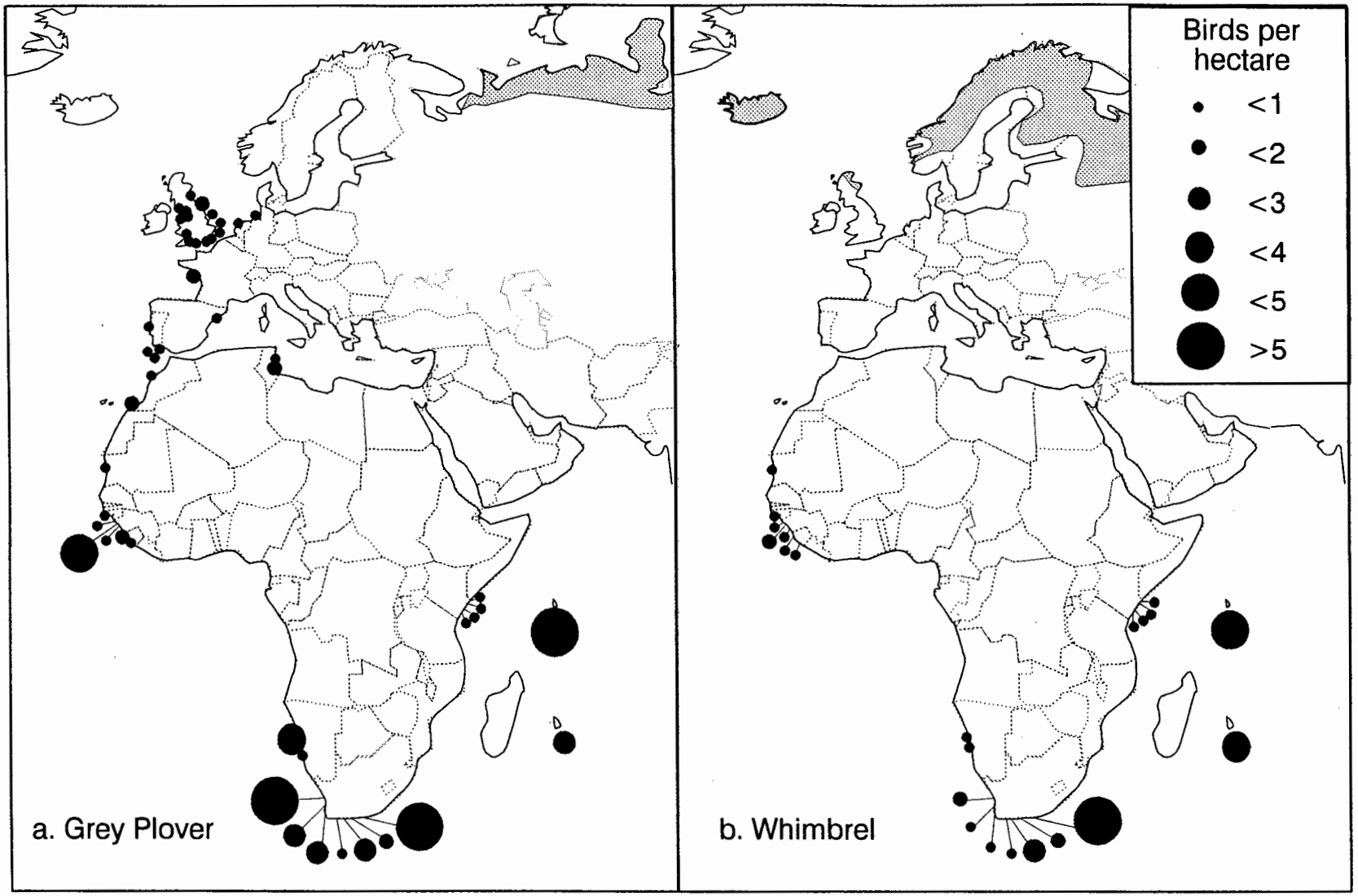


Figure 6.2. The peak nonbreeding season densities of Grey Plovers and Whimbrels at different wetlands along the eastern Atlantic and western Indian Ocean coasts (Appendix 6.2).

Table 6.1. Times of peak arrival and departure at different latitudes.

Site	Grey Plover arrival	Grey Plover departure	Whimbrel arrival	Whimbrel departure	Source
53°N Wash, U.K	Aug	May	-	-	Branson & Minton 1976
19°N Mauritania		22/4-11/5		15/4-6/5	Piersma *et al.* 1990
10°N Somalia		late Apr		late Apr	Ash 1981
3°S Kenya	late Aug -early Sep	late Apr	mid Aug -mid Sep	late Apr	Pearson & Britton 1980
33°S Berg, S.A.	Sep-Oct	April	Sep-Oct	April	Velásquez *et al.* 1991
34°S Zwartkops, S.A.	Sep-Oct	April	Sep-Oct	late Mar -April	Chapter 1, Martin 1991

Estuarine sediment type influences invertebrate distribution (McLusky 1981, Warwick *et al.* 1991) and has a strong influence on the structure of shorebird communities (Hill *et al.* 1993, Yates *et al.* 1993). Many of the large north temperate wetlands listed in Appendix 6.2 are dominated by sandy sediments (e.g. Morecambe Bay, the Wadden Sea, and the Wash; Anderson 1972, Wolf & Smit 1984, Prater 1981), whereas the smaller estuaries, such as the Tees estuary and the Solent, are predominantly muddy (Townshend 1982, Tubbs 1991). Muddier north temperate estuaries support higher densities of Grey Plovers than sandier sites; this may be due to differences in their invertebrate communities. The importance of invertebrate communities in influencing shorebird community structure is well illustrated by the differences between the similar-sized Berg and Zwartkops estuaries, South Africa. The benthic invertebrate community at the former is dominated by polychaete worms, and the shorebird community is dominated by small species (mostly Curlew Sandpipers; Kalejta 1991, Velásquez, Kalejta & Hockey 1991). At the Zwartkops estuary, the predominance of large crustaceans (Hanekom, Baird & Erasmus 1988) results in a shorebird community dominated by large species (Grey Plovers and Whimbrels; Martin 1991). Moreover, different types of prey influence the spatial requirements of visually foraging birds such as Grey Plovers (Chapters 4, 5), which in turn may influence their overall densities.

Timing of migration

Female Grey Plovers and Whimbrels usually depart first from the breeding grounds, followed by males, then juveniles (Cramp & Simmons 1983). Peak arrival times at nonbreeding sites are progressively later towards the south, and peak departure times

are progressively earlier (Table 6.1). Although some movement occurs between sites within the nonbreeding range (Dugan 1981, Evans 1981), their peak arrival and departure times suggest that Grey Plovers and Whimbrels spend less time on average at more southerly nonbreeding sites.

Morphometrics

Among Whimbrels, the most southerly (and largest) breeding race, *Numenius p. alboaxillaris*, winters mainly in East Africa, whereas the more northerly breeding races, *N. p. hudsonicus*, *N. p. variegatus*,and *N. p. phaeopus*, migrate as far south as the southern extremes of the Nearctic, Australasian and Afrotropical regions, respectively. *N. p. phaeopus* occurs sympatrically with *alboaxillaris* in East Africa (Cramp & Simmons 1983). All Whimbrels captured by mistnetting in Mauritius and South Africa in this study were identified as belonging to the nominate race. Grey Plovers lack distinct races, and it is unknown whether there is any leap-frogging between populations. There is, however, evidence of pronounced sexual differences in Grey Plover migration distance, with males comprising about 90% of European museum specimens and females making up about 90% of African specimens (Cramp & Simmons 1983, Clancey 1986).

There is no significant sexual dimorphism in the body measurements of Grey Plovers, but female Whimbrels are larger than males (Cramp & Simmons 1983). The bill-lengths of Whimbrels captured in Mauritania indicate a sex-ratio biased towards females, but those from Mauritius and South Africa do not indicate a skewed sex ratio (Fig. 6.3), suggesting that there is no strong tendency for one sex to migrate further south than the other.

A comparison of the wing lengths of adult, fully moulted Grey Plovers and Whimbrels at different sites did not reveal any consistent latitudinal trends in body size, but South African birds are among the largest for both species (Table 6.2). Wing lengths of Whimbrels (of unknown race) captured in Kenya by D.J. Pearson were shorter than the mean length reported for *alboaxillaris* (Cramp & Simmons 1983, Table 6.2), and the nominate race may therefore be prevalent in this sample.

In the New World, the mean body mass of Sanderlings during the mid-nonbreeding season over a range of latitudes was negatively correlated with average ambient temperature in January (Castro *et al.* 1992). A similar relationship is found for January weights of Grey Plovers ($n = 5$, $r = -0.89$, $P < 0.05$) and possibly for Whimbrels ($n = 3$, $r = -0.98$, $P = 0.11$) in the Palaeo-Afrotropics (Fig. 6.4). However, this relationship should be examined in a seasonal perspective. The seasonal patterns in Grey Plover and Whimbrel adult body mass are compared between different sites in Figs. 6.5 and 6.6, and the corresponding mean monthly air temperatures (°C)

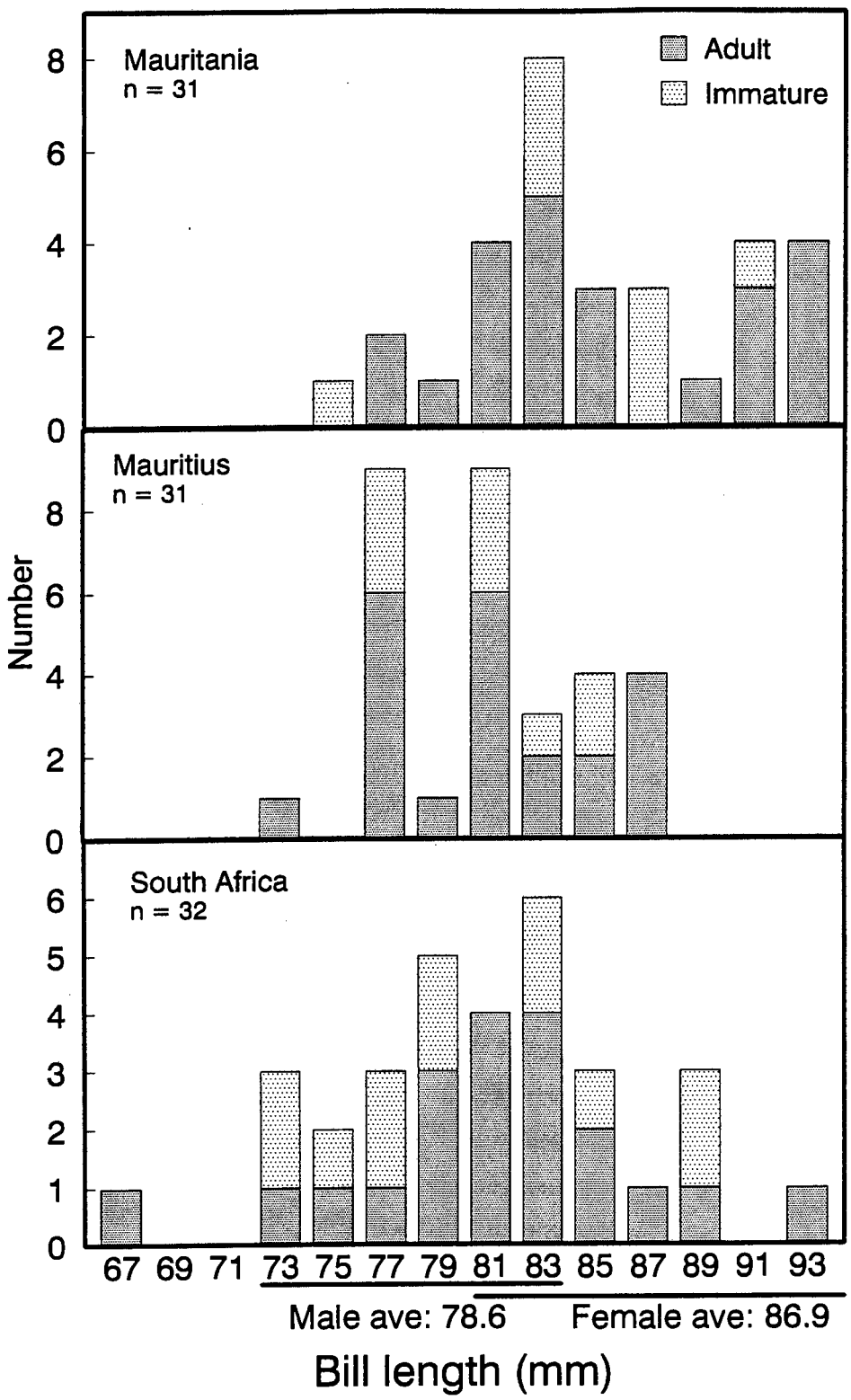


Figure 6.3. Frequency distributions of Whimbrel bill lengths measured in Mauritania (Ens *et al.* 1989), Mauritius (this study) and the Zwartkops estuary, South Africa (this study, A.P. Martin, *in litt.*). The recorded ranges and means of adult male and female bill lengths (Cramp & Simmons 1983) are shown for comparison.

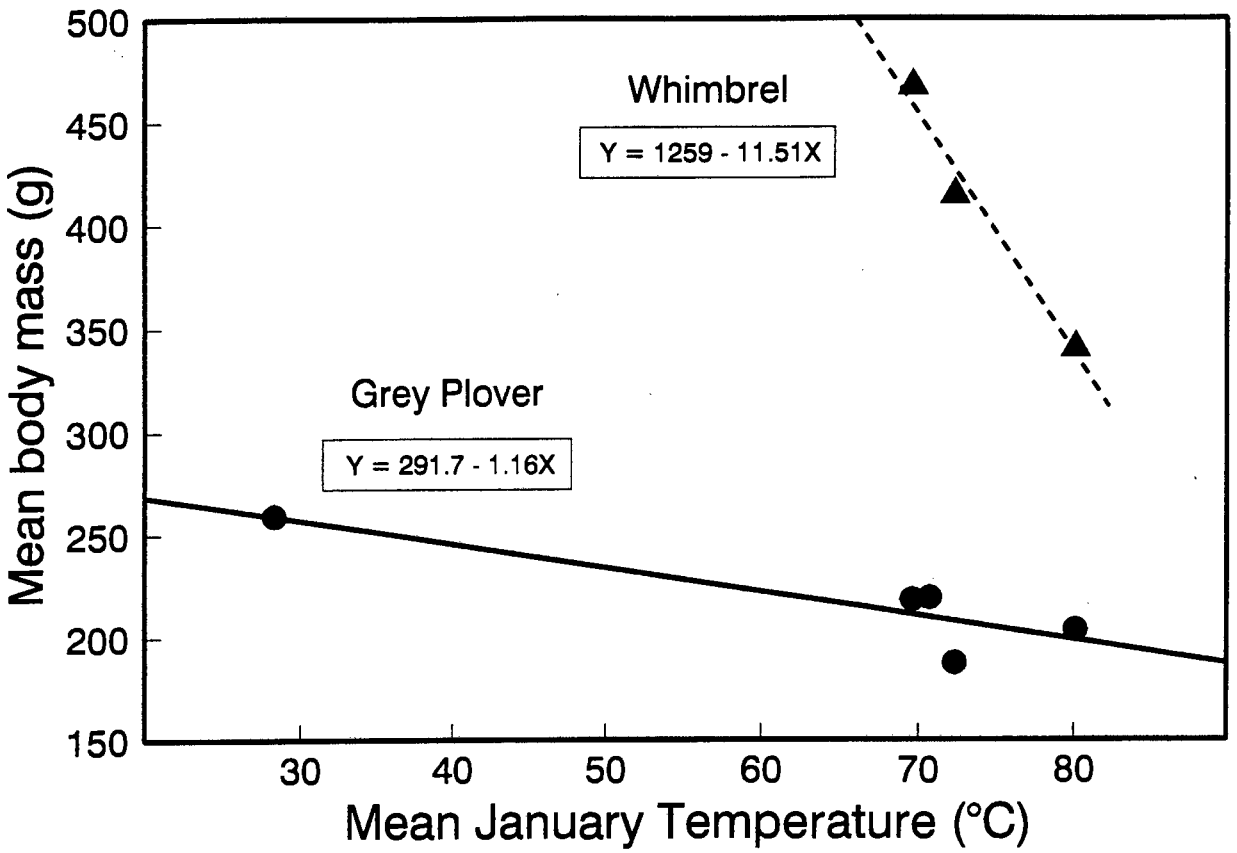


Figure 6.4. The relationships between Grey Plover and Whimbrel body mass (g) recorded in January and mean January air temperature (°C) at different sites.

Table 6.2. Mean (± S.D.) adult wing lengths (mm) of Grey Plovers and Whimbrels at different latitudes

Site		Grey Plover wing length	*n*	Whimbrel wing length	*n*	Source
53°N	The Netherlands	197 ± 4.49	55			Cramp & Simmons 1983
53°N	The Wash, U.K.	198.8 ± 5.3	1124			Branson & Minton 1976
34°N	Tunisia	204.8 198.5	25 2			Van Dijk *et al.* 1986
33°N	Morocco	201.8 ± 2.3	4			Moser 1980
19°N	Mauritania	202.4 ± 5	11			Ens *et al.* 1989
11°N	Mauritania & Guinea-Bissau	198.7 ± 4.6	59	255.8 ± 9.4	89	Zwarts *et al.* 1990c
3°S	Kenya	203.9 ± 5.6	76	245.6 ± 10.1 259*	21 35	D.J. Pearson (*in litt.*) Cramp & Simmons 1983
20°S	Mauritius	202.0 ± 7.7	19	247.9 ± 8.8	20	This study
34°S	South Africa	203.3 ± 5.2	19	252.8 ± 5.8	13	A.P. Martin (*in litt.*), this study

* *N. p. alboaxillaris*, S.D. not given.

in the different areas are shown in Fig. 6.7.

At all sites, Grey Plover body mass is low following southward migration, but it is lower at tropical and south temperate sites than in Britain (Fig. 6.5). At the Wash, Grey Plovers deposit fat and protein reserves from October to December, which they draw upon during the colder months ahead (Davidson 1981a; Fig. 6.7). The subsequent decrease in mass leaves them in poorer condition in March than when they arrived (Fig. 6.5a). At the South African sites, Grey Plovers maintain a fairly constant body mass through the first half of the residence period, followed by premigratory mass gain, which appears to take place on an equivalent time scale to that at the Wash, but a month earlier (Fig. 6.5c).

In Kenya, Grey Plovers maintained an average body mass considerably lower than at the Wash or in South Africa, thoughout most of the season (Fig. 6.5b). By April, their average body mass was only 248 g, compared with *ca.* 320 g at north and south temperate sites. It is unknown whether there was a further increase in body mass by late April, when most birds depart (Table 6.1). Grey Plovers mistnetted in Mauritius during February had an average mass which could fit the pattern found at the South African or Kenyan sites (Fig. 6.5c).

The lowest mass of Grey Plovers was recorded in West Africa in January/February, and was taken to be lean adult mass (Zwarts *et al.* 1990c). Average body mass was still very low in West Africa in comparison to other sites in March and April (Fig. 6.5b).

From December to April, Whimbrel mass was highest in South Africa, with premigratory mass averaging 580 g by March (Fig. 6.6). Whimbrels in Mauritania had a high average mass in November (Dick & Pienkowski 1979). These birds may have been staging at this site before migrating further south, or alternatively, their mass could indicate pre-midwinter reserve deposition: the activity of Whimbrels' main prey at this site, *Uca* crabs, is reduced at lower temperatures, and they remain in their burrows at temperatures below about 18°C (Zwarts 1990; see Fig. 6.7). Premigratory mass gain appears to follow a similar pattern at different latitudes, but takes place later at the tropical sites, plateauing at a much lower level for Whimbrels in Kenya. The maximum mass recorded in Kenya was 500 g (D.J. Pearson, *in litt.*), as compared with 641 g at the Zwartkops (this study) and 630 g in Mauritania (Ens *et al.* 1989).

The breeding destination of East African Grey Plovers is unknown, but at least part of the Whimbrel population in East Africa is thought to comprise the subspecies *N. p. alboaxillaris*. These birds travel a shorter distance to more southerly breeding grounds than birds migrating between southern Africa and Siberian breeding grounds. Via the great circle route, *N. p. alboaxillaris* from Kenya travel approximately 6 600 km to their breeding grounds, whereas Whimbrels from the Zwartkops estuary travel more than 11 000 km. Estimates of the flight ranges of waders vary considerably (e.g. Summers & Waltner 1979, Davidson 1984, Castro & Myers 1989). The flight range of Whimbrels with a departure mass of *ca.* 600 g and flying at 75 km/h is variously estimated to be between 4 000 and 8 000 km (Castro & Myers 1989). These formulae have been found to underestimate the known flight ranges of some shorebirds (Zwarts *et al.* 1990c), and the selective use of strong tail winds may significantly increase migratory range in some migration systems. Nevertheless, if the departure mass of Kenyan Whimbrels is as low as 500g, it suggests that their northward journey involves at least one stop-over.

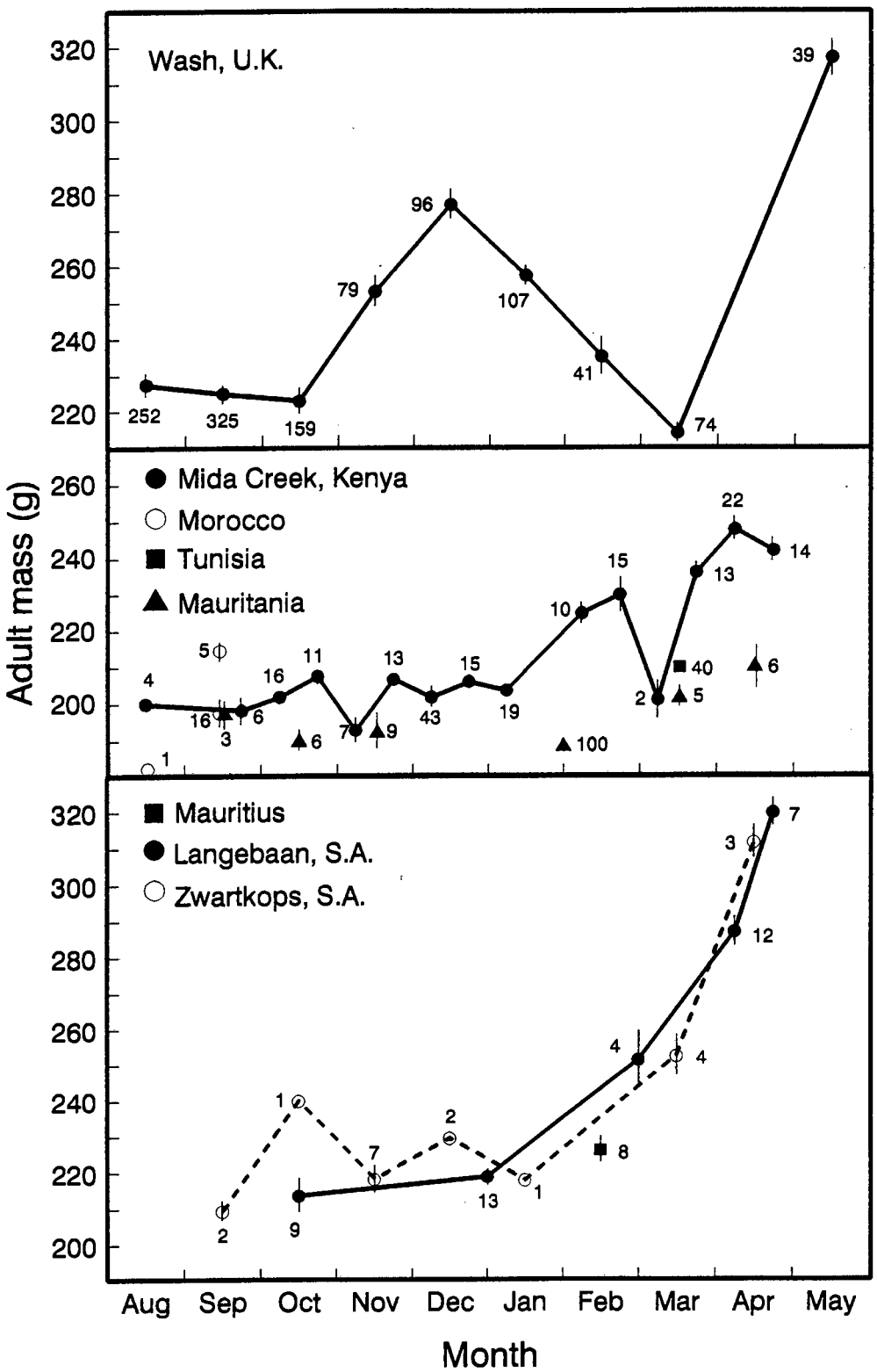


Figure 6.5. Mean (± S.E.) adult Grey Plover body mass (g) during various stages of the nonbreeding season at north temperate (the Wash, U.K. - Branson & Minton 1976; Tunisia - Van Dijk *et al.* 1986; Morocco - Dick & Pienkowski 1979, Moser 1980), tropical (Mauritania - Dick & Pienkowski 1979, Zwarts *et al.* 1990c, Ens *et al.* 1989 ; Kenya - D.J. Pearson, *in litt.*; Mauritius - this study) and south temperate sites (Langebaan, South Africa - Summers & Waltner 1979; Zwartkops estuary, South Africa - this study, A.P. Martin, *in litt.*).

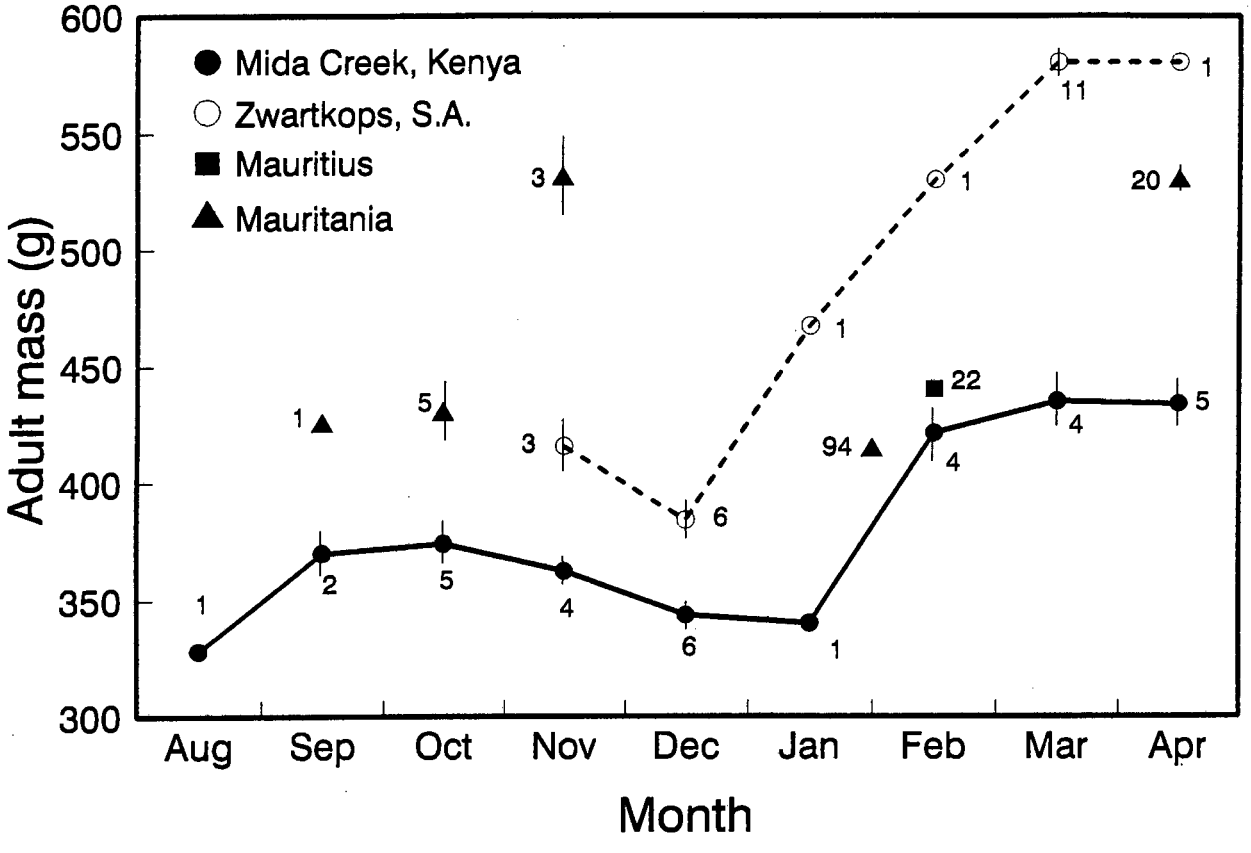


Figure 6.6. Mean (± S.E.) adult Whimbrel body mass (g) during various stages of the nonbreeding season at tropical (Mauritania - Dick & Pienkowski 1979, Zwarts *et al.* 1990c, Ens *et al.* 1989 ; Kenya - D.J. Pearson *in litt.*; Mauritius - this study) and south temperate sites (Zwartkops estuary, South Africa - this study, A.P. Martin *in litt.*).

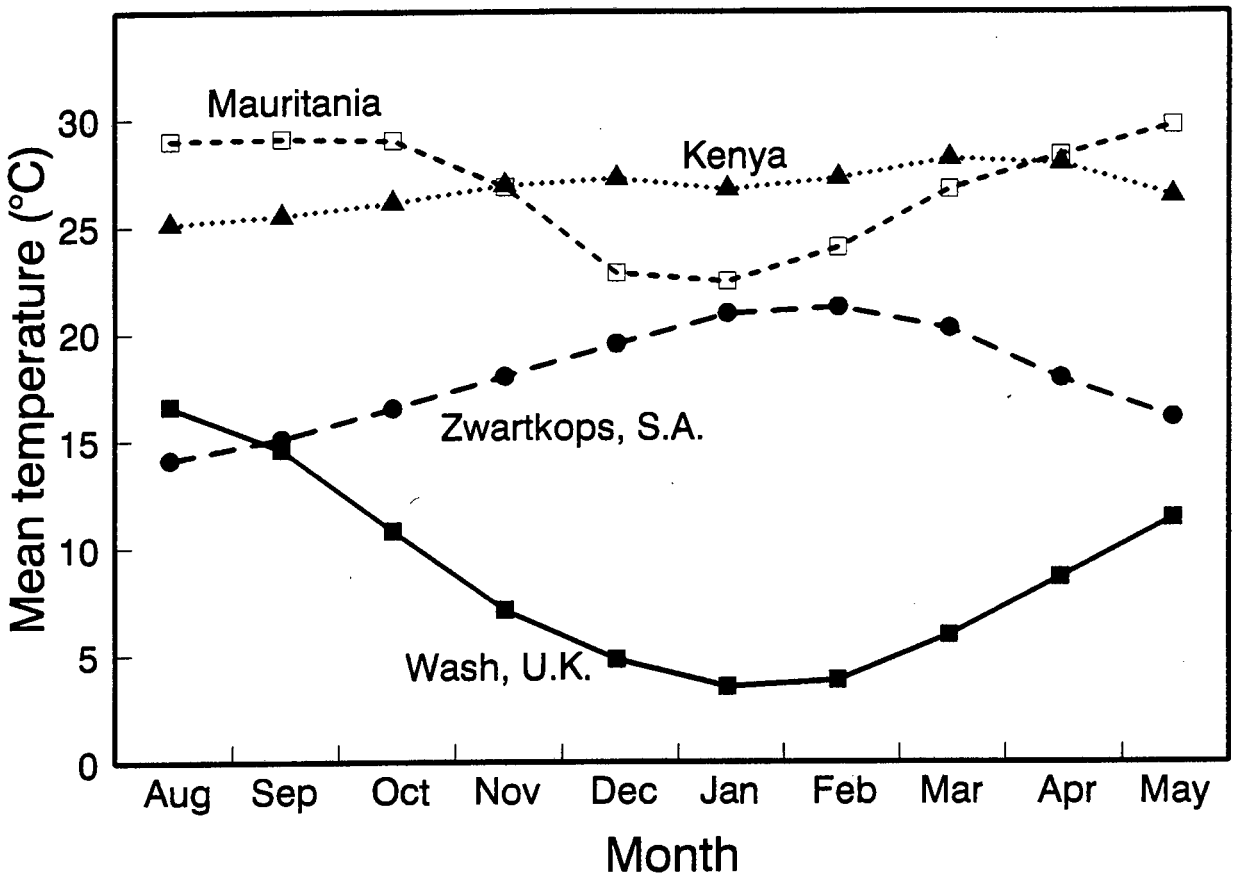


Figure 6.7. Long-term mean monthly air temperatures (°C) during the nonbreeding season at north temperate (Wash, U.K), sub-tropical (Mauritania), tropical (Kenya) and south temperate (Zwartkops, S.A.) sites (from Wernstedt 1972).

RELATIVE CONSEQUENCES OF MIGRATION TO DIFFERENT LATITUDES

Does within-winter survivorship increase towards the south?

The costs of migration are unknown (Evans & Pienkowski 1984), but it is widely assumed that *within*-'winter' survival on the nonbreeding grounds increases towards the south (Greenberg 1980, Hockey *et al.* 1992, Pienkowski & Evans 1984, Holmgren & Lundberg 1993). Empirical evidence of higher survivorship of migratory compared to resident birds (Greenberg 1980) and of longer-distance migrants (Ketterson & Nolan 1982) has been presented from a limited range within the northern hemisphere, but comparative data is lacking from a broad range of latitudes. However, ecological factors that may result in higher within-winter survivorship in the south include: (1) lower predation rates, (2) higher resource availability, and (3) increased physiological advantage (Myers *et al.* 1985) .

Predation risk

Predation by diurnal and nocturnal birds of prey (e.g. European Sparrowhawk *Accipiter nisus*, Merlin *Falco columbarius*, Peregrine Falcon *F. peregrinus*, Marsh Harrier *Circus aeruginosus*, Hen Harrier *C. cyaneus* and Short-eared Owl *Asio flammeus*) is reported to occur commonly on both European (e.g. Kus *et al.* 1984, Townshend 1984, Whitfield 1985, 1988, Mouritsen 1992) and North American wetlands (Page & Whitacre 1975, Buchanan *et al.* 1988), where they cause up to 20% mortality during the nonbreeding season in populations of some species (Whitfield 1985).

In West Africa, predation by Marsh Harriers, Lanner *F. biarmicus*, Peregrine and Barbary Falcons *F. pelegrinoides* is common (Altenburg 1982, Bijlsma 1990), and in East Africa, an average of 6 attacks by raptors per daytime low tide period (mostly by Peregrine Falcons) occurred at Mida Creek, Kenya, during March (Chapter 5).

At Tuléar, Madagascar, raptors hunted over the intertidal area less than once per week. In South Africa, African Fish Eagles *Haleaeetus vocifer*, African Marsh Harriers *C. ranivorus* and Peregrine and Lanner Falcons present the greatest threat to waders, but there was less than one raptor occurrence per day at the Berg estuary (Chapter 5, C.R. Velásquez, pers. comm.), and raptors are seen extremely rarely at the Zwartkops estuary (less than once per month; Chapter 5, A.P. Martin, pers. comm.). There was no predation threat from birds of prey in Mauritius.

These findings suggest that shorebirds are at a lower risk from predation towards the south. This may be caused by the relative abundance of birds of prey at different latitudes, as well as behavioural differences. Peregrine Falcons, for example, rarely prey on shorebirds in South Africa (A.R. Jenkins, pers. comm.). Birds of prey may specialise more on wetland birds in cold north temperate regions than in the

southern hemisphere during the boreal winter, due to their being one of the most reliable (resident within winter) and concentrated food resources: whereas birds of prey experience food shortages at inland sites during the winter in cold north temperate regions, there is no comparable situation in more southerly latitudes.

Energetic rewards

Energy intake rates vary seasonally (Chapter 1), and patterns of variation are likely to differ between sites. Therefore, a latitudinal comparison of energy intake rates should take seasonal variation into account as far as possible. Few published seasonal data on energy intake rates exist for Grey Plovers and Whimbrels, however, and in this study, the tropical sites (in Mauritius, Madagascar and Kenya) were only sampled in one month. The available data are compared in Fig. 6.8.

Grey Plovers in Britain have low energy intake rates throughout most of the residence period, and are reported to have negative energy budgets during part of the nonbreeding season (Dugan 1981, Pienkowski 1982), as exemplified by the extreme weight loss of Grey Plovers at the Wash during midwinter (Fig. 6.5a). However, their energy intake rates increase dramatically at the end of the season (May, Fig. 6.8), probably due to the onset of warmer weather and a concomitant increase in prey activity (Pienkowski 1981). Similarly, Whimbrels in Mauritania were thought to rely on an increase in prey activity in April in order to obtain sufficient food for premigratory mass deposition (Zwarts 1990). The opposite occurs at the South African sites, where intake rates are high during the first half of the season, but lower before northward migration (Fig. 6.8). Nevertheless, their lower premigratory intake rates were relatively high in comparison to those of birds further north.

Grey Plover energy intake rates were generally high at the South African sites, intermediate at tropical sites, and lowest at the north temperate sites. Too few data were available for Whimbrels to suggest any clear latitudinal pattern, and intake rates were highly variable between the southern tropical sites at the same time of year. Intake rates in Mauritania, however, were low compared to South Africa.

Physiological considerations

The negative implications of reduced energy intake rates towards the north are compounded by differences in energy requirements. Grey Plovers have a Lower Critical Temperature (LCT) of approximately 17°C (Kersten & Piersma 1987). Because Whimbrels are larger, their LCT will be lower, probably at about 12°C (Eurasian Oystercatcher *Haematopus ostralegus* (543g) LCT = 9°C; Kersten & Piersma 1987). Basal metabolic rate is constant above LCT, but increases linearly as temperature decreases below this (Kersten & Piersma 1987), thus increasing overall

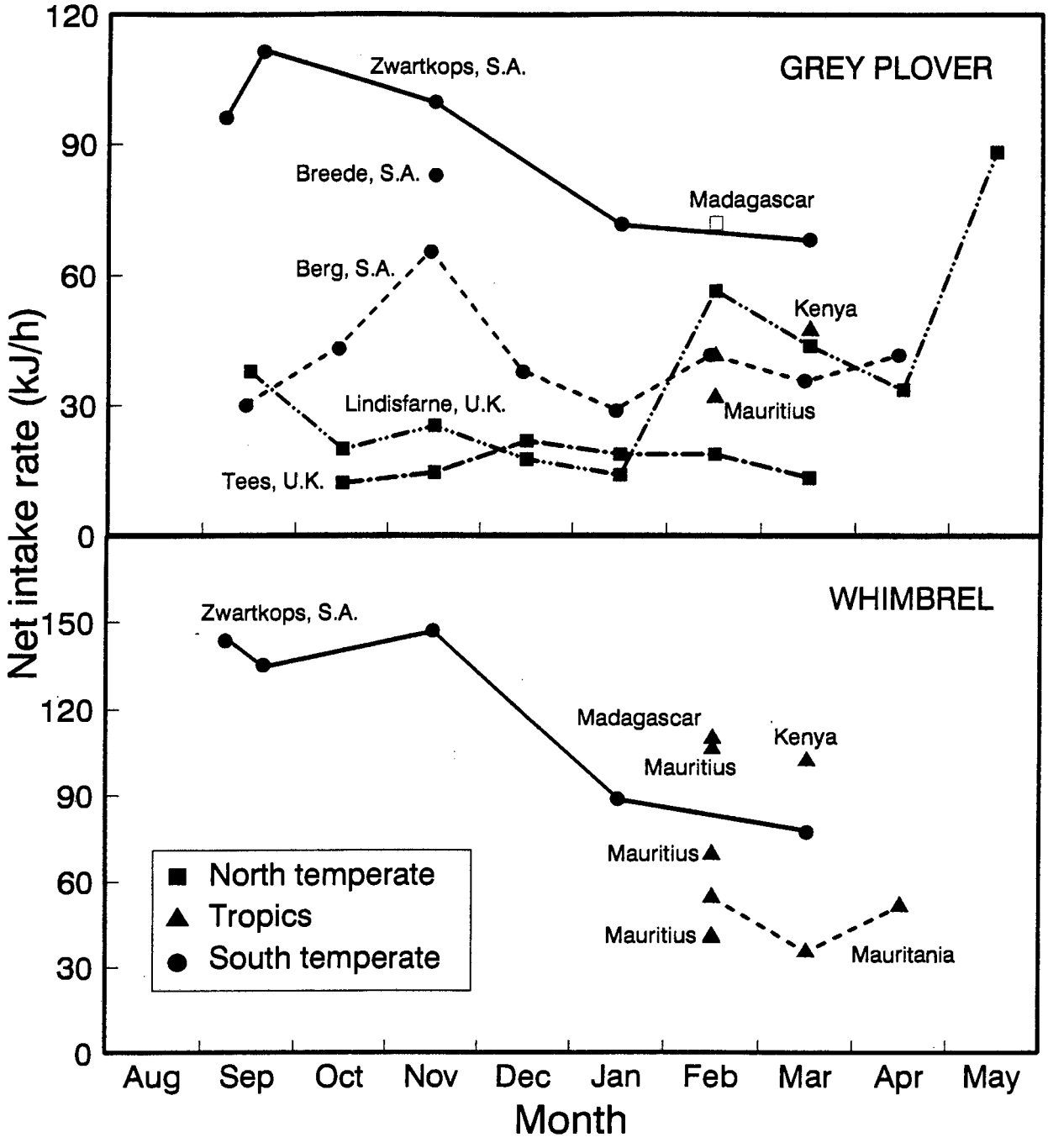


Figure 6.8. Net energy intake rates (kJ/h) of Grey Plovers and Whimbrels during various stages of the nonbreeding season at north temperate (Lindisfarne, U.K., spring tides - Pienkowski 1982; Tees, U.K. - Wood 1984), tropical (Mauritania - Zwarts & Dirksen 1990; Kenya, Mauritius, Madagascar - this study), and south temperate sites (Berg estuary, South Africa - Kalejta 1991; Breede and Zwartkops estuaries, South Africa - this study).

energetic requirements. This effect has been demonstrated latitudinally, using doubly-labelled water, for Sanderlings (*ca.* 55g), whose Daily Energy Expenditure (DEE) is negatively correlated with ambient temperature (Castro *et al.* 1992).

During the nonbreeding season, roughly August to May, average temperatures remain within the thermoneutral zone of Grey Plovers and Whimbrels throughout tropical and south temperate Africa. In Britain, temperatures remain well below LCT for Grey Plovers for most of their residence period (Pearce & Smith 1984; Fig. 6.7). There is no evidence that high temperatures in the tropics lead to heat stress, at least amongst roosting birds (Klaassen 1990).

Thus, throughout tropical and south temperate Africa, there may be no latitudinal trend in Grey Plover or Whimbrel DEE, but the southward increase in daylength may confer further an advantage to birds in south temperate regions. Grey Plovers and Whimbrels forage at night throughout their nonbreeding ranges (Chapters 3 and 4), but the thermoregulatory costs of nocturnal foraging in cold north temperate areas may be high relative to costs during the day.

In South America and Australasia, temperatures in the extreme south are low during the nonbreeding season. The southern limit of Grey Plover distribution corresponds to the 17°C January isotherm, but the larger Whimbrels occur further south (Goodall & Darby 1948, Hayman *et al.* 1986).

Fretwell's (1980) observation that density-independent factors such as temperature usually can be overcome by adaptation, is borne out in the latitudinal differences in midwinter body condition. Birds in cold climates deposit fuel reserves to survive midwinter conditions. This is further illustrated by the fact that plovers, which are more susceptible to cold weather (through the mechanism of reduced prey availability), carry larger reserves, and consequently do not have higher mortality rates, than sandpipers (Davidson 1981a,b). However, there is a trade-off between the amount of fat deposition required to survive midwinter conditions and the resultant increase in the risk of predation, which may result in birds carrying fewer reserves than would ensure survival during harsh weather (Lima 1986). The effect of inclement weather or anomalous tidal conditions is likely to be more severe for birds which have negative energy budgets, resulting in a greater risk of death from cold or starvation during midwinter. Six Grey Plovers caught at the Tees estuary in January after a period of gales weighed an average of only 137g (Dugan *et al.* 1981), and shorebird mortality during severe weather in Britain is common (e.g. Davidson 1981b, Davidson & Clark 1985, Tubbs & Wiseman 1992, Clark 1993). In Britain, it was calculated that over half of the annual mortality of many shorebird species occurs on the nonbreeding grounds, and mortality is highest during the most severe winters (Evans & Pienkowski 1984). By contrast, shorebird deaths appear to be rare on South African estuaries.

During five years of daily patrol of the Zwartkops estuary, A.P. Martin (pers. comm.) found only five dead shorebirds (including one Grey Plover). Although these findings are not formally quantified, they provide strong evidence that shorebird survivorship *on* the nonbreeding grounds is higher in the south.

Although hard evidence is not available, the above factors support the idea that within-winter survivorship increases towards the south. Data from the cold south temperate regions of the Nearctic may provide a useful comparison with regard to energetic consequences of wintering in the extreme south (Hockey *et al.* 1992). Evidence of extreme loss of body mass and starvation may provide the best means of latitudinal comparison in terms of survival advantages, but actual survivorship data from a broad range of latitudes is necessary to confirm any trends.

Is competition for resources more intense in the north?

It is frequently suggested that competition for resources among migrants is more intense at nonbreeding sites which are closest to the breeding grounds (e.g. Gauthreau 1978, Alerstam & Hogstedt 1980, Pienkowski & Evans 1985, Cox 1985). Several distributional and behavioural studies of shorebirds in the northern hemisphere suggest that resources are limited at these latitudes. The evidence cited includes the distribution of birds in relation to resources (e.g. Bryant 1979), the negative effect of bird densities on energy intake rates (e.g. Goss-Custard 1980, Ens & Goss-Custard 1984), and aggressive behaviour (Burger *et al.* 1979). Territorial defence is thought to be *prima facie* evidence for resource limitation (e.g. Terrill 1990).

The most convincing evidence of resource limitation is that of the negative effects of habitat loss on numbers of shorebirds at British wetlands (Goss-Custard 1979, Evans et al. 1979, Davidson & Evans 1986). Comparable evidence is not available from the Afrotropics, but recent large-scale reclamation at Mer Rouge, Mauritius, was thought to be part of the reason for very low energy intake rates of Grey Plovers and Whimbrels at this site (Chapter 4). Body weights of both species were lower at Mer Rouge than at Ile aux Benitiers, Mauritius, but sample sizes were too small to test whether the difference was significant (Chapter 4).

The densities of Grey Plovers and Whimbrels were frequently higher at southern African wetlands than elsewhere within the nonbreeding range (Fig. 6.2). Total shorebird carrying capacities per unit standing invertebrate biomass will be higher in the southern hemisphere, because the season of peak invertebrate production (summer) coincides with the nonbreeding season, when predation pressure from shorebirds peaks, and absolute invertebrate production is higher in warmer areas (Hockey *et al.* 1992). However the fact that bird densities are higher in the south does not provide evidence that their numbers are directly linked to carrying capacities in a constant fashion.

Moreover, the theoretical number of birds that an area can support may be held below the food limit by factors such as the amount of space required in which to forage (Goss-Custard 1985), particularly for birds which forage visually (Chapter 4). Although Grey Plovers are restricted to a stereotyped visual foraging method, they adjusted various components of this behaviour according to different types of prey taken. Whimbrels specialised on large crustaceans at all sites, and changed their foraging methods according to the habits of their prey. Consequently, the spatial requirements for foraging for each species differed between sites, and these requirements were reflected in their densities (Chapter 4). Nevertheless, the fact that densities are high in the south counters the notion that carrying capacities are more likely to be reached in more northerly than southerly wetlands.

If the depression of energy intake rates is ascribed to competitive influence, then the increase in energy intake rates towards the south (Fig. 6.8) could be construed as a consequence of reduced intensity of competition. However, the behaviour of Grey Plovers and Whimbrels at the southern limit of their Afrotropical nonbreeding ranges suggests that they experience competition of an intensity comparable to that experienced in the northern hemisphere, and that their energy requirements were not met with ease.

Both Grey Plovers and Whimbrels defend feeding territories at the northern and southern extremes of their ranges, as well as at tropical sites (Dugan 1981, 1982, Piersma & Zegers 1983, Zwarts 1990, Chapters 1, 2 and 5). This observation is contrary to Duffy, Atkins & Schneider's (1981) idea that resources are superabundant in the south (Myers & McCaffery 1984). Territorial defence occurs at intermediate levels of competition (Chapter 2), and is abandoned when competition for resources increases, as exemplified by Whimbrels at the Zwartkops estuary (Chapter 1). However, the threshold levels of competition which induce territorial behaviour and lead to its abandonment vary according to the differences in prey type between sites (Chapter 5). One of the aims of this study was to find a measurable link between agonistic behaviour and intraspecific competition, in order to allow inter-site comparisons. The problem was not adequately solved, due to the complexity of factors acting antagonistically and synergistically on individual social behaviour, but the frequency of aggressive interactions over foraging space was thought to be the most reliable indicator of competitive intensity (Chapter 5). Nevertheless, although the intensity of competition varied between the sites in this study, this does not always provide a reliable indication of the relative degree to which resources are limited at particular sites (Chapter 5).

At the Zwartkops estuary, South Africa, the distribution of Grey Plovers and Whimbrels was related to prey biomass, and their energy intake rates were negatively

influenced by conspecific density (Chapter 1). The average size of Grey Plover territories decreased during the season in direct proportion to the increase in their population, and the partitioning of spatial and food resources by territorial individuals was such that their net benefits were approximately equal (Chapter 2). Furthermore, the energetic consequences for those Grey Plovers which did not defend territories were comparatively severe; their energy intake rates were lower than those of territory holders, and decreased more rapidly during the season (Chapter 2). Although nonterritorial birds do migrate, as the only adult Grey Plovers remaining on the estuary during the austral winter were injured birds, it was suggested that their energy deficits caused a delay in their departure on northward migration. The variation in individual weights recorded during the premigratory period indicates that some birds lag behind others in terms of fat deposition. These may well represent competitively inferior individuals, although the possibility cannot be excluded that some birds migrate later to different breeding grounds. Only extensive capture and recapture programmes will establish how the body condition of nonterritorial birds progresses in comparison to territory owners.

Foraging effort by adult Grey Plovers and Whimbrels at the Zwartkops estuary did not change appreciably in response to changing energy intake rates and requirements, which suggested that birds attempted to maximise their intake rates throughout the season. Observations were carried out during spring tide periods, when the duration and extent of mudflat exposure was greatest. Daily intake may thus have been lower during neap tide periods, especially for Grey Plovers, which were unable to make use of the saltmarshes for foraging. Furthermore, both Grey Plovers and Whimbrels foraged at night thoughout the year, although energy intake rates were no higher at night than by day (Chapter 3). Grey Plovers which foraged solely on the study area achieved a total daily energy intake similar to their estimated requirements (Chapter 3).

Foraging conditions vary considerably between sites in the southern hemisphere (Chapter 4). The intensity of interference competition was a direct result of the balance between the spatial requirements for foraging and the density of conspecifics at the different sites, but the aggressive behaviour of birds did not provide a reliable indication of the overall degree to which the foraging performance of birds was influenced directly and indirectly by competition (Chapter 5). Considerations of the foraging performance of Grey Plovers and Whimbels at different sites in relation to conditions encountered strongly indicated that birds made maximal use of the time in which prey were available, and thus that resources were limited at most, if not all, of these sites through competition.

Based on the evidence in this study, I therefore suggest that competition plays

an important role in the foraging ecology of Grey Plovers and Whimbrels throughout their nonbreeding ranges, and that their densities may well be related to the carrying capacities of wetlands in a fairly constant fashion.

WHY DO SOME BIRDS MIGRATE FURTHER THAN OTHERS?

Sex differences

Male Grey Plovers, which are equal in size to females, winter furthest north, whereas there is no apparent sexual difference in migration distance of Whimbrels, of which females are the larger sex.

Several authors have offered hypotheses which could explain sexual differences in migration distance; these include (a) the dominant sex obtaining priority of access to more northerly wintering grounds (*behavioural dominance hypothesis*, Gauthreaux 1978, Ketterson & Nolan 1976, 1979), (b) the dominant sex (which establishes the breeding territory) wintering further north in order to arrive first on the breeding grounds (*arrival time hypothesis*, Ketterson & Nolan 1976, Myers 1981), or (c) the smaller sex wintering further south due to physiological limitations imposed by cold temperatures (*body size hypothesis*, Ketterson & Nolan 1979). However, none of these hypotheses can explain the full variety of observed patterns, which include larger, dominant males wintering further north (e.g. Ruff *Philomachus pugnax* - Cramp & Simmons 1983), equal-sized, dominant males wintering further north (Grey Plover - Cramp & Simmons 1983) and larger, subordinate males wintering further north (e.g. House Finch *Carpodacus mexicanus* - Belthoff & Gauthreaux 1991).

The predictions of both the *body size hypothesis* and the *behavioural dominance hypothesis* (providing dominance on the nonbreeding grounds is related to body size) are not met by either Grey Plovers or Whimbrels. In fact, the former hypothesis is now generally dismissed in terms of explaining migration patterns, because of the many examples that have been provided to the contrary (Pienkowski & Evans 1985). Furthermore, Grey Plover and Whimbrel females tend to depart earliest from the breeding grounds, which suggests either that priority of access to the best nonbreeding sites is not gained by first arrivals, or if it is, the preferred sites are not only the more northerly sites.

The patterns that occur for both Grey Plovers and Whimbrels are consistent with the predictions of the *arrival time hypothesis* (Myers 1981): male Grey Plovers arrive first and establish breeding territories on the breeding grounds, but male and female Whimbrels are highly site-faithful, tend to arrive on the breeding grounds together, often already paired and possibly mated, and nest-scraping can be initiated by either sex (Cramp & Simmons 1983).

The *arrival time hypothesis* does not, however, explain intrasexual variation in migration distance.

Long-distance migration: choice or necessity?

Competition-based hypotheses to explain migration patterns suggest that subordinate birds are forced to occupy sub-optimal habitats, or to migrate further, or both, out of 'necessity'. Greenberg (1980, 1986) proposed that migration patterns could be explained independently of competition effects, and that demographic consequences of different migratory options will lead to a 'choice' of equally advantageous 'strategies'.

Based on the relative adult survivorship and breeding productivity of resident and migratory passerines in North America, Greenberg (1980) formulated the *time-allocation* model. This model suggested that migration is most advantageous to species or populations that breed in seasonal environments, where annual breeding productivity is restricted by a short breeding season. These birds will compensate for a short breeding season by increasing their annual survivorship through migration to more benign environments. In this way, these populations would achieve equal fitness (lifetime reproductive output) to resident birds with a longer breeding season.

The *time-allocation* model has been criticised for several reasons. The model does not explain the variability in migration distance that has been found in individual shorebirds from the same breeding area (Pienkowski & Evans 1985, Evans & Davidson 1990). It has also been found, contrary to Greenberg's (1980) findings for passerines, that breeding productivity of some shorebirds is highest in the most seasonal, northerly areas, proabably due to lower predation on eggs and young (Pienkowski & Evans 1984, 1985). Cox (1985) pointed out that decreasing competition for more southerly nonbreeding areas may be the reason for their being more benign. Furthermore, Pienkowski & Evans (1985) expressed doubt as to whether habitats *are* increasingly benign towards the south, but this was based on early assessments of prey densities and energy intake rates of shorebirds in Mauritania, which have been reappraised since (Zwarts *et al.* 1990a).

The *body size competition hypothesis* asserts that, as juveniles, shorebirds settle as near to the breeding grounds as possible, but smaller birds are prevented from doing so by competition (Pienkowski & Evans 1984, 1985, Evans & Townshend 1989). The reasoning behind this hypothesis is that the cost of migration overides any possible advantage of higher within-winter survival in the south. This leads to the prediction, diametrically opposed to Greenberg's (1980), that *annual* survivorship of more southerly wintering individuals will be lower.

Cox (1985) incorporated some of the principles of Greenberg's (1980) time-allocation hypothesis into his competition theory (Cox 1968), to form the *time-*

allocation and competition hypothesis. This hypothesis has the premise that the evolution of new migratory patterns will only occur if they yield equal or improved fitness, not decreased fitness, as implied in the *body size competition hypothesis* above.

The fact that there is no latitudinal difference in body size of Whimbrels and Grey Plovers suggests that if there is a mechanism of competitive displacement, it is more likely to be based on dominance achieved through prior occupancy rather than body size (*cf.* Holmgren & Lundberg 1993). However, in species in which breeding is initiated by one sex (e.g. Grey Plover), selective pressure for that sex to winter further north than the other may be a primary determinant of migration distance of the different sexes, with dominance by prior occupancy playing a secondary role within sexes.

Although competitive interactions are likely to have been the proximate driving force for the evolution of migration patterns, the present-day nonbreeding ranges of Grey Plovers and Whimbrels have little or no room for further southward expansion, and competition is clearly not lower amongst Grey Plovers and Whimbrels in the south than in the north. Nevertheless, these birds achieve high energy intake rates in the south, and, coupled with their relatively low thermoregulatory costs and low predation risk, this provides compelling evidence that the costs of migration are balanced by higher survivorship for birds migrating furthest south. Thus an original 'necessity' of long-distance migration has probably evolved into an equally favourable 'choice' for these birds. This is further suggested by the evidence of adaptations to different migratory destinations, such as the timing and degree of reserve deposition, the timing and duration of moult (Pienkowski & Evans 1984), high site fidelity in the south as well as the north (Myers, Schick & Castro 1986, this study) and the heritability of migration routes, including long-distance routes (Berthold & Querner 1981). Moreover, the fact that Grey Plovers occupy very cold areas in the north of their nonbreeding range, but do not occur further south than the 17°C (Grey Plover LCT) January isotherm, suggests that net energetic gains in the extreme south cannot outweigh the high costs in getting there.

In conclusion, I suggest that the geographical limits to the nonbreeding range are those within which migrants can balance the costs of migration with survival advantages, and that competition for resources may be equally intense throughout this range. This is consistent with the fact that Grey Plovers and Whimbrels have high energy intake rates in the south, but competition for these resources is high.

IMPLICATIONS FOR CONSERVATION

Recent population decreases of several shorebird species have been attributed to alteration or loss of breeding habitats (Cramp & Simmons 1983), as well as extreme weather conditions (Boyd 1992), suggesting that shorebird populations may be regulated on the breeding grounds. In addition to the alteration of breeding habitats, the large-scale destruction of wetland habitats occupied by shorebirds during the nonbreeding season (e.g. Senner & Howe 1984, Larson 1991, Hollis & Jones 1991) is now thought to be a major contributing factor to the population reductions of several shorebird species (Myers 1983, Myers *et al.* 1987).

Wetlands are under increasing threat from development. It is thus important to understand whether the alteration of these habitats leads to the mortality of birds, or whether the birds can respond to changing conditions by adjusting to the reduced area, or by moving elsewhere (Evans & Dugan 1984, Goss-Custard 1985).

Evidence from this study suggests that Grey Plover and Whimbrel habitats are saturated throughout their nonbreeding ranges, although the increase in the population of Grey Plovers in Britain in recent decades (Moser 1988) may provide evidence to the contrary. Moser (*op. cit.*) proposed that the carrying capacities of several estuaries have only been reached since an increase in the Grey Plover population occurred, implying that this population increase was a result of ecological release on the breeding grounds. In South Africa, the composition of migratory shorebird populations has changed dramatically during the past century (Hockey & Douie, in press), and these changes are reflected in the proportional occurrence of different wader species at the Zwartkops estuary. At the turn of the century, Curlews *Numenius arquata* and Ringed Plovers *Charadrius hiaticula* were common, and Whimbrels and Grey Plovers were relatively rare (Brown 1905). The opposite is true at present (Underhill & Cooper 1984, Martin 1991). The decrease in numbers of Curlews since the 1950's has been ascribed to a loss of breeding habitat (Cramp & Simmons 1983), and this also may be true for Ringed Plovers. These population decreases, and possibly those of other species, probably facilitated the increase in numbers of Grey Plovers and Whimbrels, due to ecological release on the *nonbreeding grounds*.

In support of Morse (1980), I suggest that shorebird populations can be regulated on the nonbreeding as well as the breeding grounds, but fluctuating environmental conditions may lead to temporal shifts in the area of limitation. Populations may be limited on the breeding grounds by years of high predation (e.g. the cyclical shifts in predation pressure from Arctic foxes *Alopex lagopus* - Summers & Underhill 1987) or the delayed onset of boreal spring. Fluctuations in shorebird and prey populations are unlikely to be synchronous, and population regulation on the

nonbreeding grounds may only occur on a significant scale in years in which bumper breeding production is coupled with severe weather or low invertebrate productivity on the nonbreeding grounds. Nevertheless, an *a priori* assumption that shorebird habitats are currently saturated throughout their ranges will lead to the safest possible conservation strategies.

Although the actual numbers of shorebirds that reach South Africa are low due to habitat availability, the findings of this study indicate that habitats in the south are as valuable to shorebirds as those further north (*contra* Pienkowski & Evans 1985). The fact that shorebird densities at these sites are high (Hockey *et al.* 1992, this study) means that larger numbers of shorebirds can be conserved per unit area of wetland in southern hemisphere wetlands than in those further north. Moreover, the conservation of migrants at the extremes of their ranges is important in terms of retaining the genetic diversity that exists within these broad-ranging species. In South Africa, the prioritization of conservation sites for Grey Plovers and Whimbrels is particularly easy, as 55% and 40%, respectively, of their total populations in this country occur at two wetlands, Langebaan Lagoon and the Zwartkops estuary.

Appendix 6.1. Numbers of Whimbrels and Grey Plovers per coastal country on Palaeo-Afrotropical flyways during the nonbreeding season.

Country	Grey Plover	Whimbrel	Source
Denmark	100		a
Germany	2 000		a
Netherlands	9 700		a
Belgium	100		a
Ireland	1 200		a
Great Britain	21 300		a
France	2 000		a
Spain	3 600	400	a
Portugal	6 800		a
Italy	1 800		a
Tunisia	20 500		a
Morocco	4 000	600	a
Canary Islands	800	300	a
Mauritania	19 300	18600	a
Senegal	1 500	3 000	b
Gambia	100	1 000	a
Guinea-Bissau	56 700	41 500	a
Guinea		'1 000's'	f
Sierra-Leone	11 600	6 200	g
Liberia	300	1 200	a
Ghana	1 717	477	c
Namibia	6 000	234	d
South Africa	8 000	3 100	d
Tanzania	21000	18000	e
Kenya	4600	2250	d
Sudan	1000	500	d
Egypt	7-1300	'few'	d
Saudi Arabia	7 000	'few'	h

a: Smit & Piersma 1989; b: Meininger 1989; c: Ntiamoa-Baidu & Grieve 1987; d: Summers *et al.* 1987; e: Bregnballe *et al.* 1990; f: Altenberg & van der Kamp 1989; g: extrapolated from Tye & Tye 1987; h: Zwarts, Felemban & Price 1991.

Appendix 6.2. Number of Grey Plovers and Whimbrels wintering in different wetlands, in relation to latitude. Area (ha) is, as far as possible, intertidal area, excluding saltmarsh area.

Latitude	Wetland	Area (ha)	Grey Plover n	Grey Plover n/ha	Whimbrel n	Whimbrel n/ha	Sources (area, counts)
55°41'N	Lindisfarne, U.K.	3 278	150	*0.046*			a, b
54°38'N	Teesmouth, U.K.	200	350	*1.750*			c, d
54°07'N	Morecambe B., U.K.	28 967	230	*0.008*			c
54°N	German Wadden	220 000	1 300	*0.006*			e, f
53°50'N	Ribble, U.K.	8 500	770	*0.091*			g, b
53°31'N	Alt, U.K.	500	190	*0.380*			h, b
53°18'N	Dee, U.K.	11 420	1 600	*0.140*			a, i
53°N	Dutch Wadden	120 000	2 500	*0.021*			j, i
52°58'N	Wash, U.K.	27 000	4 200	*0.156*			i, i
51°57'N	Stour, U.K.	1 600	405	*0.253*			a, b
51°30'N	Severn, U.K.	19 700	500	*0.025*			c, l
51°29'N	Thames, U.K.	4 800	2 800	*0.583*			h, i
51°48'N	Netherlands Delta	30 000	7 200	*0.240*			l, i
51°21'N	Swale, U.K.	9 102	2 000	*0.220*			h, i
50°49'N	Solent, U.K.	6 920	5 517	*0.797*			m
50°46'N	Pagham, U.K.	300	185	*0.617*			h, b
50°37'N	Exe, U.K.	1 080	280	*0.259*			a, b
46°N	Vendee, France	4 500	5 900	*1.311*			l
40°42'N	Ebro Delta, Spain	16 700	600	*0.036*			n
38°48'N	Tagus, Portugal	12 000	5 055	*0.421*			j, o
37°02'N	Fusetta, Portugal	24	11	*0.458*			o
37°07'N	Tavira, Portugal	74	33	*0.446*			o
37°13'N	Castro Marim, Portugal	372	93	*0.250*			o
34°50'N	Merja Zerga, Morocco	2 200	2 000	*0.909*			p
34°22'N	Kneiss, Tunisia	14 600	12 566	*0.861*			q
33°40'N	Gourine, Tunisia	1 600	1 836	*1.148*			q
32°52'N	Oualida/Sidi, Morocco	1 000	800	*0.800*			h, p
28°N	Puerto Cansado, Morocco	3 000	3 000	*1.000*			p
19°N	Banc d'Arguin, Mauritania	54 000	19 300	*0.357*	18 600	*0.344*	j, i
11°N	Guinea-Bissau	156 800	56 700	*0.362*	41 500	*0.265*	j
10°50'N	Katchek, Guinea	40	34	*0.850*	18	*0.450*	s, r
10°35'N	Kamsar, Guinea	65	260	*4.000*	99	*1.523*	r
09°30'N	Kobayah, Guinea	750	315	*0.420*	263	*0.351*	r

Appendix 6.2 continued

08°30'N	Sierra-Leone River	1 800	2 300	*1.278*	1100	*0.611*	s
08°N	Yawri Bay, Sierra-Leone	9 100	3 500	*0.385*	2000	*0.220*	s
03°30'S	Sabaki estuary, Kenya	75	15	*0.200*	13	*0.173*	i
03°22'S	Mida Creek, Kenya	580	560	*0.966*	250	*0.431*	i
10°S	Mtwapa Creek, Kenya	41	8	*0.195*	8	*0.195*	i
10°S	Bamburi Beach, Kenya	337	24	*0.071*	11	*0.033*	i
5°S	Victoria Flats, Seychelles	9	52	*5.778*	39	*4.333*	i, t
20°08'S	Mer Rouge, Mauritius	20	50	*2.500*	71	*3.550*	u
23°S	Walvis Bay, Namibia	800	2 479	*3.100*	13	*0.016*	v
23°20'S	Sandwich, Namibia	1 300	900	*0.692*	12	*0.009*	s, v
31°42'S	Olifants, S. Africa	66	330	*5.000*	66	*1.000*	w
32°47'S	Berg, S. Africa	143	310	*2.168*	49	*0.343*	x
33°10'S	Langebaan, S. Africa	1 700	3 615	*2.124*	441	*0.259*	j
33°52'S	Zwartkops, S. Africa	104	810	*7.788*	784	*7.538*	y
34°20'S	Gouritz, S. Africa	11	31	*2.818*	26	*2.364*	w
34°24'S	Breede, S. Africa	150	71	*0.473*	54	*0.360*	w
34°36'S	UilKraals, S. Africa	40	67	*1.675*	65	*1.625*	w

a: Hockey *et al.* (1992); b: Prater (1981); c: Dugan (1980); d: Townshend *et al.* (1984); e: Zwarts (1981); f: Prokosch (1984); g: Smith & Greenhalgh (1977); h: Scott (1980); i: Smit & Piersma (1989); j: Zwarts (1988); h: Bryant (1980); l: Smit (1981); m: Tubbs (1991); n: Vilalta (1985); o: Bijlsma *et al.* (1985); p: Kersten & Smit (1984); q: Van Dijk *et al.* (1986); r: Altenburg & van der Kamp (1989); s: Tye & Tye (1987); t: Feare & High (1977); u: This study; v:; Whitelaw *et al.* (1978); w: Ryan *et al.* (1988); x: Velásquez *et al.* (1991); y: Martin 1991.

SUMMARY

1. Little is known of the consequences of long distance migration and of why some birds migrate further than others. Hypotheses to explain variation in migration distance are largely based on assumptions about the relative survivorship of birds migrating different distances and about latitudinal differences in the intensity of competition for resources. Most work on shorebirds has been carried out in the northern hemisphere, and comparatively little is known of the ecology of broad-ranging migrants in the southern parts of their nonbreeding ranges. The main aims of this study were to provide comparative data on the foraging ecology of broad-ranging migrants in the southern hemisphere, particularly at the southern limits of their nonbreeding ranges, in order to determine the relative benefits and the importance of competition to birds 'wintering' at these latitudes. The foraging ecology of Grey Plovers *Pluvialis squatarola* (Charadriidae) and Whimbrels *Numenius phaeopus* (Scolopacidae) was investigated at several sites in the southern hemisphere. These species breed at high north temperate and polar latitudes and migrate south to spend the boreal winter on the coasts of all the continents, except Antarctica, from north temperate to south temperate latitudes.

2. Plovers have a stereotyped visual foraging method, whereas sandpipers (Scolopacidae) forage visually or tactilely. The behaviour of Grey Plovers suggested that their 'run-stop-search' foraging method is a result of low visual acuity whilst moving. Despite this stereotypy, Grey Plovers at different sites altered their foraging speed and the area that they searched according to the nature of their prey. The extent to which Whimbrels foraged visually or tactilely at different sites was dependent on the behaviour and microhabitats of their prey. Spatial requirements for foraging thus differed between sites, and the differences were more extreme for Whimbrels than for Grey Plovers. Grey Plovers appeared to have an upper limit to their foraging densities, imposed by their foraging behaviour, but Whimbrels foraged at high densities when foraging tactilely. Because of the versatility in their behaviour, Whimbrels were able to be more specialised than Grey Plovers in prey choice.

3. The main influx of Grey Plovers and Whimbrels to the Zwartkops estuary, South Africa, occurred in September, and their numbers continued to increase until the middle of the austral summer. During the austral winter, immature birds remained on the estuary. Mudprawns *Upogebia africana* dominate the invertebrate biomass at the Zwartkops estuary, and move to the surface during low tide, an unusual behaviour which is thought to be parasite-induced. About 90% of the low tide energy intake of both species was provided by these mudprawns, which were captured almost exclusively on the surface, and small crabs *Cleistostoma* spp. made up most of the

remainder. Immature Grey Plovers and Whimbrels occupied the richest sections of the estuary during winter, and in spring, these sections were occupied first by the newly arriving migrants, resulting in the displacement of some immature birds to other parts of the estuary. The distribution of both species on the estuary during summer was related to the biomass of *Upogebia*. During the low tide period, the number of Whimbrels on the study area corresponded to both the state of tidal exposure and tidal changes in the availability of mudprawns. Grey Plovers remained on fixed feeding territories for the full duration of tidal exposure.

4. The availability (numbers surfacing) of mudprawns and number of crabs at the Zwartkops estuary is higher during the austral summer than in winter. During winter, immature Grey Plovers had low energy intake rates, and Whimbrels obtained a greater proportion of their prawn catch by tactile means. During the nonbreeding season, the energy intake rates of both species were unrelated to patterns of prey availability, but were negatively influenced by increasing conspecific density. Grey Plovers foraged for about 55 - 75%, and Whimbrels for 50 - 65% of the time of tidal exposure. Most of the remaining low tide time was probably required for digestive pauses, but there was evidence that foraging activity was suppressed at very high bird densities. The daily energy requirements of Grey Plovers and Whimbrels were estimated from the measurements of birds captured on the estuary at different stages of the nonbreeding season. Except during spring, when energy intake rates were highest, neither species was able to satisfy its daily requirements during the daytime low tide period. Whimbrels achieved a lower proportion of their daily requirements than Grey Plovers during low tide, but also foraged in the saltmarshes at mid tide, where their activities could not be quantified. Both species foraged at night throughout the year.

5. During the premigratory period (March), Grey Plovers and Whimbrels had the lowest intake rates of the season and both species foraged as much at night as during the day. Grey Plovers occupied the same feeding territories as during the day, but Whimbrels tended to forage closer together. Although both species continued to forage visually at night, they exhibited behavioural changes to compensate for the reduced visibility. Both foraged more slowly at night, taking fewer steps per minute, and Grey Plovers paused for longer to search for prey. Prey items were sighted from shorter distances at night than during the day, and fewer small prey were eaten at night. Energy intake rates, however, did not differ significantly by day and night for either species, and both achieved over 40% of their daily low-tide period intake at night. Total low tide intake by Grey Plovers, which fed exclusively on the study area, was similar to their predicted energy requirements, but Whimbrels obtained only about 75%

of their requirements during the low tide period, and presumably obtained the balance in the saltmarshes.

6. Inter- and intraspecific competition were thought to play important roles in the foraging ecology of both Grey Plovers and Whimbrels at the Zwartkops estuary. Evidence included the large overlap in the diets of the two species, their distribution along the estuary in relation to prey biomass, the negative influence of bird density on energy intake rates, and the constancy of foraging effort throughout the nonbreeding season despite changes in energy intake rates and requirements.

7. The foraging effort and performance of the two species were compared at several tropical and south temperate sites during the premigratory period. Prey types and tidal exposure time varied markedly between sites, as did bird densities and energy intake rates. There were no consistent trends between any of these factors, but the proportion of the tidal exposure time for which birds foraged during the daytime was similar at most sites, and birds foraged nocturnally at all the sites that were visited at night. Instantaneous daytime energy intake rates of both species were frequently high at sites where tidal exposure duration was short, and low at sites where exposure duration was long. High daytime intake rates also were achieved by Whimbrels at three sites where tidal exposure was fairly long. These included the only two sites at which fiddler crabs were the main prey. Fiddler crabs may be more difficult to catch at night, resulting in lower overall energy intake rates. At the site with the longest exposure time, Whimbrels achieved high energy intake rates, but foraged for the shortest proportion of the available time. This may be because their prey were unavailable at certain times during tidal exposure, due to temperature- (or dessication-) related rhythms in their activity. Both species had low energy intake rates at a site where tidal exposure duration was fairly short, but a large area of this site had recently been reclaimed. On the basis of these findings, it was suggested that birds made maximal use of the time in which prey were available, at least during the premigratory period, constrained only by the intervals required for digestion. It was concluded that access to resources was limited by competition.

8. Many Whimbrels established large feeding territories on the Zwartkops estuary during the spring arrival period, but these were abandoned as their numbers increased further. During the low tide period, aggression rates were highest when the study area was first exposed. During the nonbreeding season, aggression rates were highest during the spring arrival period, and were fairly constant thereafter, despite increased densities of birds and competition for resources. These patterns were attributed to the

compounding influence of the establishment of social hierarchies and neighbour familiarisation. Aggressive encounter rates were higher during March 1990 than during the following summer, when the density of conspecifics was lower.

9. A large proportion of Grey Plovers established feeding territories during the spring arrival period and retained them throughout the residence period. The average size of territories decreased during the season in relation to the total population of Grey Plovers on the estuary, rather than in response to prey availability. Average rates of territorial encounters decreased through the season, probably due to neighbour familiarity. Furthermore, the direction of movement of birds in relation to one another indicated the active avoidance of aggressive encounters. Territory size was inversely related to resource density. The holders of smaller territories were involved in aggressive encounters more frequently than holders of larger territories. Owners of large territories had lower energy intake rates and foraged for longer than owners of small territories. These patterns suggested that the net benefits to territory owners were approximately equal, and there was no evidence of a dominance hierarchy amongst territory holders. Nonterritorial birds achieved lower energy intake rates than territory holders and their energy intake rates decreased more rapidly through the season. It is probable that these birds were delayed in their departure on northward migration. Like territory holders, nonterritorial Grey Plovers comprised both adult and immature birds. Evidence suggested that nonterritorial birds were competitively inferior.

10. The aggressive behaviour of Grey Plovers and Whimbrels varied considerably between sites, even at the same time of year. Both species were territorial at some sites but not others, but there was no consistent relationship between the occurrence of this behaviour and prey type, energy intake rates, bird densities or predation risk. The levels of competition at which territorial defence occurs probably vary according to the nature of the prey base. Nonterritorial aggression was dominated by chases, and a higher proportion of chases were aerial when the distance between birds was greatest. Interspecific aggression was relatively uncommon, and, whereas few intraspecific encounters involved food items, most interspecific encounters were kleptoparasitic. Kleptoparasitism occurred opportunistically at sites where large prey were eaten and at sites where energy intake rates were lowest. The frequency of kleptoparasitic encounters was dependent on the frequency of opportunities for this behaviour, determined by prey size and the availability of potential hosts, and was thus not considered to be a good indicator of competition. The frequency of intraspecific encounters over foraging space was a function of conspecific density, search area and foraging speed. The rate of these encounters thus provided a reliable indicator of the

level of interference, despite the variation in their nature and duration. However, this study demonstrated that inter-site differences in the overall effects of competition on the foraging performance of individuals could not be inferred from aggressive behaviour alone.

11. During the nonbreeding season, the absolute numbers of Grey Plovers and Whimbrels are highest in the northern hemisphere, but their densities are frequently higher at southerly wetlands than in the north. It has been suggested that carrying capacities of wetlands are highest in the south. Several factors indicate that survival of migrants on the nonbreeding grounds is also highest in the south. The risk of predation decreases towards the south; energy intake rates of Grey Plovers and Whimbrels are generally highest in the south and lowest in the northern hemisphere; energy requirements are likely to be higher at north temperate latitudes than in tropical and south temperate Africa; and, shorebirds are at greater risk from starvation in the cold north temperate regions. These patterns, coupled with the evidence for the prevalence of competition at tropical and south temperate sites, suggest that, although competition probably played a role in the evolution of migration patterns, birds migrating further south balance the costs of migration with higher survival rates on the nonbreeding grounds, and competition for resources at these sites is no less intense than at sites closer to the breeding grounds. This further suggests that the present day nonbreeding ranges of Grey Plovers and Whimbrels are 'saturated', and that population regulation occurs on the nonbreeding grounds, even in the south. This, and the fact that bird densities are high in the south, has important ramifications for the development of conservation strategies.

REFERENCES

ABRAMSON, M. 1979. Vigilance as a factor influencing flock formation among Curlews *Numenius arquata*. *Ibis* **121**: 213-216.

ALERSTAM, T. & HOGSTEDT, G. 1980. Spring predictability and leap-frog migration. *Ornis Scand.* **11**: 196-200.

ALI, S. & RIPLEY, S.D. 1969. *Handbook of the birds of India and Pakistan* 2. Bombay: Oxford University Press.

ALTENBURG, W. 1982. Avifauna. *In*: Altenburg, W., Engelmoer, M., Mes, R. & Piersma, T. *Wintering waders on the Banc d'Arguin, Mauritania.* Report of the Netherlands Ornithological Mauritanian Expedition, 1980.

ALTENBURG, W. & VAN DER KAMP, J. 1989. Coastal waders in Guinea. *Wader Study Group Bull.* **54**: 33-35.

ALTEROGT, R. & DAVIS, T.A. 1980. Nocturnal activity of the Turnstone *Arenaria interpres* on South Sentinel (Andaman Islands). *J. Bombay Nat. Hist. Soc.* **77**: 508-510.

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**: 227-265.

ANDERSON, S.S. 1972. The ecology of Morecambe Bay II. Intertidal invertebrates and factors affecting their distribution. *J. Appl. Ecol.* 9: 161-178.

ASH, J.S. 1981. Spring passage of Whimbrel *Numenius phaeopus* and other waders off the coast of Somalia. *Scopus* **5**: 71-76.

ASHKENAZIE, S. & SAFRIEL, U.N. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* **60**: 783-799.

BAKER, J.M. 1981. Winter feeding rates of Redshank *Tringa totanus* and Turnstone *Arenaria interpres* on a rocky shore. *Ibis* **123**: 85-87.

BAKER, M.C. 1974. Foraging behaviour of Black-bellied Plovers (*Pluvialis squatarola*). *Ecology* **55**: 162-167.

BAKER, M.C. & BAKER, A.E.M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monogr.* **43**: 193-212.

BELL, H.L. & FORD, H.A. 1990. The influence of food shortage on interspecific niche overlap and foraging behaviour of three species of Australian warblers (Acanthizidae). *In*: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper Ornithological Society.

BELTHOFF, J.R. & GAUTHREAUX, S.A. 1991. Partial migration and differential winter distribution of house finches in the eastern United States. *Condor* **93**: 374-382.

BENT, A.C. 1962. *Life histories of North American Shore Birds*, Part 1. New York: Dover Publications.

BENNETT, S.E. 1980. Interspecific competition and the niche of the American Redstart

(*Setophaga ruticulla*) in wintering and breeding communities. *In*: Keast, A. & Morton, E.S. (eds). *Migrant birds in the Neotropics: ecology, behaviour, distribution and conservation.* Washington: Smithsonian Institution Press.

BERTHOLD, P. & QUERNER, U. 1981. Genetic basis of migratory behaviour in European warblers. *Science* **212**: 77-79.

BIJLSMA, R.G. 1990. Predation by large falcon species on wintering waders on the Banc d'Arguin, Mauritania. *Ardea* **78**: 75-82.

BIJLSMA, R.G., MEININGER, P.L., REKERS, M., DE RODER, F.E., SCHULTING, R. & VOGEL, R. 1985. Wader counts in the Tejo eestuary near Lisbon and in the salinas of south Portugal. *Wader Study Group Bull.* **43**: 23-24.

BOLAND, J.M. 1990. Leapfrog migration in North American shorebirds: intra- and interspecific examples. *Condor* **92**: 284-290.

BOYD, H. 1992. Arctic summer conditions and British Knot numbers: an exploratory analysis. *Wader Study Group Bull.* **64**, *Suppl.*: 144-152.

BRANSON, N.J.B.A. & MINTON, C.D.T. 1976. Moult, measurements and migrations of the Grey Plover. *Bird Study* **23**: 257-266.

BREGNBALLE, T., HALBERG, K., HANSEN, L.N., PETERSEN, I.K. & THORUP, O. 1990. Ornithological winter surveys on the coast of Tanzania 1988-1989. *ICBP Study Report* **43**: 1-63.

BROWN, J.G. 1905. Notes on the waterbirds of the Zwartkops River, Port Elizabeth, Cape Colony. *J. S. Afr. Onith. Union* **1**: 39-48.

BROWN, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**: 160-169.

BROWN, J.L. 1969. Territorial behaviour and population regulation in birds. *Wilson Bull.* **81**: 293-329.

BRYANT, D.M. 1979. Effects of prey density and site character on estuary usage by overwintering waders. *Estuar. Coast. Mar. Sci.* **9**: 369-384.

BRYANT, D.M. 1980. Waders on the coast of Kenya: January 1979. *Wader Study Group Bull.* **28**: 28-30.

BRYANT, D.M. & WESTERTERP, K.R. 1980. Energetics of foraging and free existence in birds. *Proc. Int. Orn. Congr.* **17**: 292-299.

BUCHANAN, J.B., SCHICK, C.T., BRENNAN, L.A. & HERMAN, S.G. 1988. Merlin predation on wintering Dunlins: hunting success and Dunlin escape tactics. *Wilson Bull.* **100**: 108-118.

BURGER, J. 1984. Abiotic factors affecting migrant shorebirds. *In* Burger, J. & Olla, B.L. (eds.) *Behaviour of Marine Animals*, Vol. 6. Shorebirds: Migration and Foraging Behaviour: 1-72. New York & London: Plenum Press.

BURGER, J., HAHN, D.C., & CHASE, J. 1979. Aggressive interactions in mixed-species

flocks of migrating shorebirds. *Anim. Behav.* **27**: 459-469.

CARPENTER, F.L. 1987a. Introduction to the symposium: Territoriality: conceptual advances in field and theoretical studies. *Amer. Zool.* **27**: 223-228.

CARPENTER, F.L. 1987b. The study of territoriality: complexities and future directions. *Amer. Zool.* **27**: 401-409.

CASTRO, G. & MYERS, J.P. 1989. Flight range estimates for shorebirds. *Auk* **106**: 474-476.

CASTRO, G., MYERS, J.P. & RICKLEFS, R.E. 1992. Ecology and energetics of sanderlings migrating to four latitudes. *Ecology* **73**: 833-844.

CHRISTIE, N.D. & MOLDAN, A. 1977. Distribution of benthic macrofauna in Langebaan Lagoon. *Trans. roy. Soc. S. Afr.* **42**: 273-284.

CLANCEY, P.A. 1986. Comments of the Grey Plover in Natal. *Albatross* **288**: 8-9.

CLARK, C. & MANGEL, M. 1984. Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **109**: 626-641.

CLARK, N.A. 1993. Wash Oystercatchers starving. *Wader Study Group Bull.* **70**: 51-52.

CLARKE, T.A. 1970. Territorial behaviour and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda. Ecol. Monogr.* **40**: 189-212.

COX, G.W. 1968. The role of competition in the evolution of migration. *Evolution* **22**: 180-192.

COX, G.W, 1985. The evolution of migration systems between temperate amd tropical regions of the new world. *Am. Nat.* **126**: 451-474.

CRAMP, S. & SIMMONS, K.E.L. (eds). 1983. *The Birds of the Western Palearctic*, Vol. 3. Oxford: Oxford University Press.

DANN, P. 1986. *The ecology of birds feeding in intertidal areas in Southern Victoria.* PhD. Thesis, University of Melbourne.

DARE, P.J. & MERCER, A.J. 1973. Foods of the Oystercatcher in Morecambe Bay, Lancashire. *Bird Study* **20**: 173-184.

DAVIDSON, N.C. 1981a. *Seasonal changes in nutritional conditions of shorebirds during the nonbreeding season.* Ph.D. thesis. University of Durham.

DAVIDSON, N.C. 1981b. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. *In*: Jones, N.V. & Wolff, W.J. *Feeding and survival strategies of estuarine organisms*. London: Plenum Press.

DAVIDSON, N.C. 1984. How valid are flight range estimates for waders? *Ring. & Migr.* **5**: 49-64.

DAVIDSON, N.C. & CLARK, N.A. 1985. The effects of severe weather in January and February 1985 on waders in Britain. *Wader Study Group Bull.* **44**: 10-15.

DAVIDSON, N.C. & EVANS, P.R. 1986. The role and potential of man-made and man-

modified wetlands in the enhancement of the survival of overwintering shorebirds. *Colonial Waterbirds* **9**: 176-188.

DAVIDSON, N.C. & PIERSMA, T. The migration of Knots: conservation needs and implications. *In*: Piersma, T. & Davidson, N.C. (eds). The migration of Knots. *Wader Study Group Bull.* **64**, Suppl.:198-209.

DAVIDSON, P.E. 1967. A study of the Oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fish. Invest., Lond. Ser. II.* **25**: 1-28.

DAVIDSON, P.E. 1968. The Oystercatcher - a pest of shellfisheries. *In* Murton, R.K. & Wright, E.N. (eds). *The Problems of Birds as Pests*: 141-155. New York: Academic Press.

DAVIES, N.B. 1978. Ecological questions about territorial behaviour. *In*: Krebs, J.R. & Davies, N.B. (eds). *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell Scientific Publications.

DAY, J.H. 1981. Summaries of current knowledge of 43 estuaries in southern Africa. *In*: Day, J.H. (ed). *Estuarine ecology with particular reference to southern Africa*. Rotterdam: A.A. Balkema.

DICK, W.J.A. & PIENKOWSKI, M.W. 1979. Autumn and early winter weights of waders in north-west Africa. *Ornis Scand.* **10**: 117-123.

DIT DURELL, S.E.A. LE V., & KELLY, C.P. 1990. Diets of Dunlin *Calidris alpina* and Grey Plovers *Pluvialis squatarola* on the Wash as determined by dropping analysis. *Bird Study* **37**: 44-47.

DRENT, R. & PIERSMA, T. 1990. An exploration of the energetics of leap-frog migration in Arctic breeding waders. *In*: Gwinner, E. (Ed.) *Bird migration*. Berlin: Springer-Verlag.

DRINNAN, R.E. 1957. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the cockle (*Cardium edule*). *J. Anim. Ecol.* **26**: 439-467.

DRINNAN, R.E. 1958a. Observations on the feeding of the Oystercatcher in captivity. *Brit. Birds* **51**: 139-149.

DRINNAN, R.E. 1958b. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, north Wales. *Fish. Invest., Lond. Ser. II.* **22**: 1-15.

DUFFY, D.C., ATKINS, N. & SCHNEIDER, D.C. 1981. Do shorebirds compete on their wintering grounds? *Auk* **98**: 215-229.

DUGAN, P.J. 1980. *Seasonal movements of shorebirds in relation to prey availability and spacing behaviour.* Ph.D. thesis, University of Durham.

DUGAN, P.J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. *In* Jones, N.V. & Wolff, W.J. (eds).

Feeding and Survival Strategies of Estuarine Organisms: 251-260. New York: Plenum Press.

DUGAN, P.J. 1982. Seasonal changes in patch use by a territorial Grey Plover: weather-dependent adjustments in foraging behaviour. *J. Anim. Ecol.* **51**: 849-857.

DUGAN, P.J., EVANS, P.R. GOODYER, L.R. & DAVIDSON, N.C. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. *Ibis* **123**: 359-363.

ELS, S. 1982. *Distribution and abundance of two crab species on the Swartkops estuary saltmarshes and the energetics of the* Sesarma catenata *population.* MSc Thesis, University of Port Elizabeth.

ENGELMOER, M., PIERSMA, T., ALTENBURG, W. & MES, R. 1984. The Banc d'Arguin (Mauritania) In P.R. Evans, J.D. Goss-Custard & W.G. Hale (eds.) *Coastal waders and wildfowl in winter*: 272-292. Cambridge University Press, Cambridge.

ENS, B.J. & GOSS-CUSTARD, J.D. 1984. Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *J. Anim. Ecol.* **53**: 217-231.

ENS, B.J., PIERSMA, T. WOLFF, W.J. & ZWARTS, L. 1989. *Report of the Dutch-Mauritanian project, Banc d'Arguin 1985-1986.* WIWO report no. 25.

ESSELINK, P. & ZWARTS, L. 1989. Seasonal trends in burrow depth and tidal variation in feeding activity of Nereis diversicolor. *Mar. Ecol. Prog. Ser.* **56**: 243-254.

EVANS, P.R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution and movement in the non-breeding season. *Ardea* **64**: 117-139.

EVANS, P.R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. In: Naylon, E. & Hartnoll, R.G. (eds.) *Cyclic phenomena in marine plants and animals*: 357-366. Oxford: Pergamon Press.

EVANS, P.R. 1981. Migration and dispersal of shorebirds as a survival strategy. *In*: Jones, N.V. & Wolff, W.J. (eds). *Feeding and survival strategies of estuarine organisms*. London: Plenum Press.

EVANS, P.R. 1984. Introduction. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter.* Cambridge: Cambridge University Press.

EVANS, P.R. & DAVIDSON, N.C. 1990. Migration strategies and tactics of waders breeding in Arctic and north temperate latitudes. *In*: Gwinner, E. (ed). *Bird migration.* Berlin: Springer-Verlag.

EVANS, P.R. & DUGAN, P.J. 1984. Coastal birds: numbers in relation to food

resources. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter*. Cambridge: Cambridge University Press.

EVANS, P.R., HERDSON, D.M., KNIGHTS, P.J. & PIENKOWSKI, M.W. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. I. Shorebird diets, invertebrate densities, and the impact of predation on the invertebrates. *Oecologia* **41**: 183-206.

EVANS, P.R. & TOWNSHEND, D.J. 1989. Site faithfulness of waders away from the breeding grounds: how individual migration patterns are established. *Proc. 19th Int. Ornithol. Congr. (Ottawa)*. pp. 594-603.

FEARE, C.J. & HIGH, J.H. 1977. Migrant shorebirds in the Seychelles. *Ibis* **119**: 323-338.

FEDAK, M.A., PINSHOW, B. & SCHMIDT-NIELSEN, K. 1974 Energy cost of bipedal running. *Amer. J. Physiol.* **227**: 1038-1044.

FLEISCHER, R.C. 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging and vigilance behaviour. *Condor* **85**: 22-29.

FRETWELL, S.D. 1980. Evolution of migration in relation to factors regulating bird numbers. *In*: Keast, A. & Morton, E.S. (eds). *Migrant birds in the Neotropics: ecology, behaviour, distribution, and conservation*. Washington: Smithsonian Institution.

GASS, C.L. 1979. Territory regulation, tenure and migration in Rufous Hummingbirds. *Can. J. Zool.* **57**: 914-923.

GASS, C.L., ANGEHR, G. & CENTA, J. 1976. Regulation of food supply by feeding territoriality in the Rufous Hummingbird. *Can. J. Zool.* **54**: 2046-2054.

GAUTHREAUX, S.A. 1978. The ecological significance of behavioural dominance. *In*: Bateson, P.P.G. & Klopfer, P.H. (eds). *Perspectives in ethology*. New York: Plenum Press.

GETTY, T. 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbours form defensive coalitions? *Amer. Zool.* **27**: 327-336.

GIBB, J. 1957. Food requirements and other observations on captive tits. *Bird Study* 4: 207-215.

GILL, F.B. & WOLF, L.L. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology*. **56**: 333-345.

GOCHFELD, M. 1971. Notes on a nocturnal roost of Spotted Sandpipers in Trinidad, West Indies. *Auk* **88**: 167-168.

GOODALL, G. & DARBY, H.C. 1948. *The university atlas*. London: George Philip & Son.

GOSS-CUSTARD, J.D. 1969. The winter feeding ecology of the Redshank *Tringa totanus*. *Ibis* **111**: 338-356.

GOSS-CUSTARD, J.D. 1970. Feeding dispersion in some overwintering wading birds. *In* Crook, J.H. (ed) *Social Behaviour in Birds and Mammals*: 3-335. New York: Academic Press.

GOSS-CUSTARD, J.D. 1976. Variation in the dispersion of Redshank, *Tringa totanus*, on their winter feeding grounds. *Ibis* **118**: 257-263.

GOSS-CUSTARD, J.D. 1977a. Predator responses and prey mortality in Redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas) *J. Anim. Ecol.* **46**: 21-35.

GOSS-CUSTARD, J.D. 1977b. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *J. appl. Ecol.* **14**: 721-739.

GOSS-CUSTARD, J.D. 1979. Effect of habitat loss on the numbers of overwintering shorebirds. *Studies in Avian Biol.* **2**: 167-177.

GOSS-CUSTARD, J.D. 1980. Competition for food and interference among waders. *Ardea* **68**: 31-52.

GOSS-CUSTARD, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: Sibly, R.M & Smith, R.H. (eds). *Behavioural ecology*: 169-188. Oxford: Blackwell Scientific Publications.

GOSS-CUSTARD, J.D. & DIT DURRELL, S.E.A.LE V. 1988. The effect of dominance and feeding method on the intake rates of Oystercatchers, *Haematopus ostralegus*, feeding on mussels. J. Anim. Ecol. 57: 827-844.

GOSS-CUSTARD, J.D, JONES, R.E. & NEWBERY, P.E. 1977a. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *J. appl. Ecol.* **14**: 681-700.

GOSS-CUSTARD, J.D., KAY, D.G. & BLINDELL, R.M. 1977b. The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. *Est. Coast. Mar. Sci.* **5**: 497-510.

GOSS-CUSTARD, J.D. & MOSER, M. 1988. Rates of change in the number of dunlin, Calidris alpina, wintering in British estuaries in relation to the spread of *Spartina anglica*. *J. Appl. Ecol.* **25**: 95-109.

GREENBERG, R. 1980. Demographic aspects of long-distance migration. *In*: Keast, A. & Morton, E.A. (eds). *Migrant birds in the Neotropics: ecology, behaviour, distribution and conservation.* Washington: Smithsonian Institution.

GREENBERG, R. 1986. Competition in migrant birds in the nonbreeding season. *Curr. Ornithol.* **3**: 281-307.

GREENBERG, R. 1990. Ecological plasticity, neophobia, and resource use in birds. *In*: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper

Ornithological Society.

GREENHALGH, M.E. 1975. *Studies on the foods and feeding ecology of wading birds.* PhD. Thesis, Liverpool Polytechnic.

GÜNTHER, H.J. 1963. Untersuchungen zur Verbreitung und ökologie von *Uca tangeri* an der SW-Iberischen Kuste. *Z. Morph. Ökol. Tiere* **53**: 242-310.

GUTIERREZ, A.L. & DOMINGUEZ, J.G. 1991. An observation of Whimbrel Numenius phaopus feeding on fish. *Wader Study Group Bull.* **61**: 27.

HALE, W.G. 1980. *Waders*. London: Collins.

HAMILTON, W.J. 1959. Aggressive behaviour in migrant Pectoral Sandpipers. *Condor* **61**: 161-179.

HANEKOM, N. 1980. *A study of two thalassinid prawns in the non* Spartina *regions of the Swartkops estuary*. Ph.D. thesis, University of Port Elizabeth.

HANEKOM, N. & ERASMUS, T. 1988. Variations in size compositions of populations of *Upogebia africana* (Ortmann) (Decapoda, Crustacea) within the Zwartkops estuary and possible influencing factors. *S. Afr. J. Zool.* **23**: 259-265.

HANEKOM, N.M., BAIRD, D. & ERASMUS, T. 1988. A quantitative study to assess standing biomasses of macrobenthos in soft substrata of the Swartkops Estuary, South Africa. *S. Afr. J. Mar. Sci.* **6**: 163-174.

HARRINGTON, B.A. & GROVES, S. 1977. Aggression in foraging migrant Semipalmated Sandpipers. *Wilson Bull.* **89**: 336-338.

HAYMAN, P., MARCHANT, J. & PRATER, A.J. 1986. *Shorebirds: an Identification Guide to the Waders of the World.* London & Sydney: Croom Helm.

HEPPLESTON, P.B. 1970. Anatomical observations on the bill of the Oystercatcher (*Haematopus ostralegus occidentalis*) in relation to feeding behaviour. *J. Zool., Lond.* **161**: 519-524.

HEPPLESTON, P.B. 1971. The feeding ecology of Oystercatchers *Haematopus ostralegus* L. in winter in northern Scotland. *J. Anim. Ecol.* **41**: 651-672.

HICKLIN, P.W. & SMITH, P.C. 1979. The diets of five species of migrant shorebirds in the Bay of Fundy. *Proceedings of the Nova Scotian Institute of Science* **29**: 483-488.

HILL, D., RUSHTON, S.P., CLARK, N., GREEN, P. & PRYS-JONES, R. 1993. Shorebird communities on British estuaries: factors affecting community composition. *J. Appl. Ecol.* **30**: 220-234.

HINDE, R.A. 1970. *Animal behaviour: a synthesis of ethology and comparative psychology*. 2nd edition. New York: McGraw-Hill.

HOCKEY, P.A.R. 1984. Behaviour patterns of non-breeding African Black Oystercatchers *Haematopus moquini* at offshore islands. *Proc. Pan-Afr. Orn. Congr.* **5**: 707-727.

HOCKEY, P.A.R. 1985. Observations on the communal roosting of African Black Oystercatchers. *Ostrich* **56**: 52-57.

HOCKEY, P.A.R., NAVARRO, R.A., KALEJTA, B. & VELASQUEZ, C.R. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *Am. Nat.* **140**: 961-979.

HOCKEY, P.A.R. & STEELE, W.K. 1989. Intraspecific kleptoparasitism and foraging efficiency as constraints on food selection by Kelp Gulls Larus dominicanus. *In*: Hughes, R.N. (ed) *Behavioural mechanisms of food selection*. Berlin: Springer-Verlag.

HOCKEY, P.A.R. & UNDERHILL, L.G. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *S. Afr. J. Zool.* **19**: 1-11.

HOLLIS, G.E. & JONES, T.A. 1991. Europe and the Mediterranean Basin. *In*: Finlayson, M. & Moser, M. (eds). *Wetlands*. Oxford: Facts on File.

HOLMGREN, N. & LUNDBERG, S. 1993. Despotic behaviour and the evolution of migration patterns in birds. *Ornis Scand.* **24**: 103-109.

HULSCHER, J.B. 1974. An experimental study of the food intake of the Oystercatcher *Haematopus ostralegus* L. in captivity during the summer. *Ardea* **62**: 155-171.

HULSCHER, J.B. 1976. Localization of cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* **64**: 292-310.

HULSCHER, J.B. 1982. The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* **70**: 89-152.

HUTTO, R.L. 1990a. Studies of foraging behaviour: central to understanding the ecological consequences of variation in food abundance. *In*: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper Ornithological Society.

HUTTO, R.L. 1990b. Measuring the availability of food resources. *In*: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper Ornithological Society.

JACKSON, S. 1990. *Seabird digestive physiology in relation to foraging ecology.* Ph.D. thesis, University of Cape Town.

JOHNSON, O.W., JOHNSON, P.M. & BRUNER, P.L. 1981. Wintering behaviour and site-faithfulness of Golden Plovers on Oahu. *`Elepaio* **41**: 123-130.

KALEJTA, B. 1991. *Aspects of the ecology of migrant shorebirds (Aves: Charadrii) at the Berg River estuary, South Africa.* Ph.D. thesis, University of Cape Town.

KALEJTA, B. & HOCKEY, P.A.R. 1991. Distribution, abundance and productivity of

benthic invertebrates at the Berg River estuary, South Africa. *Estuar., Coastal & Shelf Sci.* **33**: 175-191.

KERSTEN, M. & PIERSMA, T. 1984. Voedselkeuze en voedselopname van Zilverplevieren *Pluvialis squatarola* in de Waddenzee tijdens voor- en najaarstrek. *Limosa* **57**: 105-111.

KERSTEN, M. & PIERSMA, T. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**: 175-187.

KERSTEN, M. & SMIT, C.J. 1984. The Atlantic coast of Morocco. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter*. Pp. 276-292. Cambridge: Cambridge University Press.

KETTERSON, E.D. & NOLAN, V. 1976. Geographic variation and its climatic correlates in the sex ratios of eastern-wintering Dark-eyed Juncos. *Ecol.* **57**: 679-693.

KETTERSON, E.D. & NOLAN, V. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). *Auk* **96**: 532-536.

KETTERSON, E.D. & NOLAN, V. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. *Auk* **99**: 243-259.

KETTERSON, E.D. & NOLAN, V. 1983. The evolution of differential bird migration. *In*: Johnston, R.F. (ed) *Current Orniothology*, Vol. 1, pp. 357-402. New York: Plenum Press.

KLAASSEN, M. 1990. Short note on the possible occurrence of heat stress in roosting waders on the Banc d'Arguin, Mauritania. *Ardea* **78**: 63-65.

KODRIC-BROWN, A. & BROWN, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* **59**: 285-296.

KREBS, J.R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology* **52**: 2-22.

KREBS, J.R. 1980. Optimal foraging, predation risk and territory defence. *Ardea* **75**: 175-187.

KREBS, J.R. & DAVIES, N.B. 1981. *An introduction to behavioural ecology*. Oxford: Blackwell Scientific Publications.

KUS, B.E., ASHMAN, P., PAGE, G.W. & STENZEL, L.E. 1984. Age-related mortality in a wintering opopulation of Dunlin. *Auk* **101**: 67-73.

LACK, D. 1968. Bird migration and natural selection. *Oikos* **19**: 1-9.

LACK, D. & LACK, P. 1972. Wintering warblers in Jamaica. *Living Bird* **11**: 129-153.

LARSON, J.S. 1991. North America. *In*: Finlayson, M. & Moser, M. (eds). *Wetlands*.

Oxford: Facts on File.

LIFJELD, J.T. 1984. Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. *Ornis Scand.* **15**: 217-226.

LIMA, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**: 377-385.

LINDSTROM, A. & PIERSMA, T. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**: 70-78.

MACARTHUR, R.H. 1969. Species packing, and what interspecies competition minimises. *Proc. Nat. Acad. Sci.* **64**: 1369-1371.

MACLEAN, S.F., JR. & SEASTEDT, T.R. 1979. Avian territoriality: sufficient resources or interference competition. *Am. Nat.* **114**: 308-312.

MACNAE, W. 1957. The ecology of the plants and animals in the intertidal regions of the Zwartkops estuary near Port Elizabeth, South Africa. Part 1. *J. Ecol.* **45**: 113-131.

MALLORY, E.P. 1981. *Ecological, behavioural and morphological adaptations of a shorebird (the Whimbrel,* Numenius phaeopus hudsonicus) *to its different migratory environments.* Ph.D. thesis, Dartmouth College, Hanover.

MALLORY, E.P. 1982. Territoriality of Whimbrels *Numenius phaeopus hudsonicus* wintering in Panama. *Wader Study Group Bull.* **34**: 135-139.

MARTIN, A.P. 1991. *Feeding ecology of birds on the Swartkops estuary, South Africa.* PhD thesis, University of Port Elizabeth.

MARTIN, A.P. & BAIRD, D. 1988. Lemming cycles - which Palearctic migrants are affected? *Bird Study* **35**: 143-145.

MASCHER, J.W. 1966. Weight variations in resting Dunlin (*Calidris a. alpina*) on autumn migration in Sweden. *Bird-banding* **37**: 1-34.

MCLUSKY, D.S. 1981. *The estuarine ecosystem.* Glasgow: Blackie.

MCNEIL, R. 1991. Nocturnality in shorebirds. *Proc. Int. Orn. Congr.* **20**: 1098-1104.

MCNEIL, R. & ROBERT, M. 1988. Nocturnal feeding strategies of some shorebird species in a tropical environment. *Proc. Int. Orn. Congr.* **19**: 2328-2336.

MEININGER, P.L. 1989. Palearctic coastal waders wintering in Senegal. *Wader Study Group Bull* **55**: 18-19.

METCALFE, N.B. & FURNESS, R.W. 1984. Changing priorities: the effect of premigratory fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociobiol.* **15**: 203-206.

METCALFE, N.B. & FURNESS, R.W. 1987. Aggression in shorebirds in relation to flock density and composition. *Ibis* **129**: 553-563.

MOERMOND, T.C. 1990. A functional approach to foraging: morphology, behaviour, and the capacity to exploit. *In*: Morrison, M.L., Ralph, C.J., Verner, J. &

Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper Ornithological Society.

MORRIER, A. & MCNEIL, R. 1991. Time-activity budget of Wilson's and Semipalmated Plovers in a tropical environment. *Wilson Bull.* **103**: 598-620.

MORRISON, R.I.G. & ROSS, R.K. 1989. *Atlas of Nearctic shorebirds on the coast of South America.* Canadian Wildlife Service, Ottawa.

MORSE, D.H. 1980a. *Behavioural mechanisms in ecology.* Harvard University Press, Cambridge.

MORSE, D.H. 1980b. Population limitation: breeding or wintering grounds? *In*: Keast, A. & Morton, E.S. (eds) *Migrant birds in the Neotropics: behaviour, distribution and conservation.* Washington: Smithsonian Institution Press.

MOSER, M.E. 1980. *Shorebird studies in north west Morocco.* Durham: Durham University.

MOSER, M.E. 1988. Limits to the number of Grey Plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long-term population trends. *J. Appl. Ecol.* **25**: 473-485.

MOURITSEN, K.N. 1992. Predator avoidance in night-feeding Dunlins Calidris alpina: a matter of concealment. *Ornis Scand.* **23**: 195-198.

MYERS, J.P. 1980. Territoriality and flocking by Buff-breasted Sandpipers: variations in non-breeding dispersion. *Condor* **82**: 241-250.

MYERS, J.P. 1981. A test of three hypotheses for latitudinal segregationof the sexes in wintering birds. *Can. J. Zool.* **59**: 1527-1534.

MYERS, J.P. 1983. Conservation of migrating shorebirds: staging areas, geographical bottlenecks and regional movements. *Am. Birds* **37**: 23-25.

MYERS, J.P. 1984. Spacing behaviour of nonbreeding shorebirds. *In*: Burger, J. & Olla, B.L. (eds). *Shorebirds: migration and foraging behaviour*: 271-321. New York: Plenum Press.

MYERS, J.P. & MCCAFFERY, B.J. 1984. Paracas revisited: do shorebirds compete on their wintering ground? *Auk* **101**: 197-199.

MYERS, J.P. & MYERS, L.P. 1979. Shorebirds of coastal Buenos Aires Province, Argentina. *Ibis* **121**: 186-200.

MYERS, J.P., CONNORS, P.G. & PITELKA, F.A. 1979a. Territoriality in non-breeding shorebirds. *Avian Biol.* **2**: 231-246.

MYERS, J.P., CONNORS, P.G. & PITELKA, F.A. 1979b. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk* **96**: 551-561.

MYERS, J.P., CONNORS, P.G. & PITELKA, F.A. 1981. Optimal territory size and the Sanderling: compromises in a variable environment. *In*: Kamil, A.C & Sargent,

T.D. (eds). *Foraging behaviour: ecological, ethological and psychological approaches*: 135-158. New York: Garland STPM Press.

MYERS, J.P., MARON, J.L. & SALLABERRY, M. 1985. Going to estremes: why do sanderings migrate to the neotropics? *Orn. Monogr.* **36**: 520-535.

MYERS, J.P., MORRISON, R.I.G., ANTAS, P.Z., LOVEJOY, T.E., SALLABERRY, M., SENNER, S.E. & TARAK, A. 1987. Conservation strategy for migratory species. *Am. Scientist* **75**: 18-26.

MYERS, J.P., SCHICK, C.T. & CASTRO, G. 1986. Structure in Sanderling (*Calidris alba*) populations: the magnitude of intra- and interyear dispersal during the nonbreeding season. *In*: Ouellet, H. (ed). *Proc. 19th Int. Orn. Congr. (Ottawa)*: 604-615.

MYERS, J.P., WILLIAMS, S.L. & PITELKA, F.A. 1980. An experimental analysis of prey availability for Sanderlings *Calidris alba* Pallas feeding on sandy beach crustaceans. *Can. J. Zool.* **58**: 1564-1574.

NAGY, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**: 111-128.

NEWTON, I. 1980. The role of food in limiting bird numbers. *Ardea* **68**: 11-30.

NTIAMOA-BAIDU, Y. & GRIEVE, A. 1987. Palearctic waders in coastal Ghana in 1985/86. *Wader Study Group Bull.* **49**, Suppl./IWRB Special Publ. **7**: 76-78.

PAGE, G. & WHITACRE, D.F. 1975. Raptor predation on wintering shorebirds. *Condor* **77**: 73-83.

PATON, D.C. & CARPENTER, F.L. 1984. Peripheral foraging by territorial Rufous Hummingbirds: defense by exploitation. *Ecology* **65**, 1808-1819.

PEARCE, E.A. & SMITH, C.G. 1984. *The world weather guide*. London: Hutchinson.

PEARSON, D.J. & BRITTON, P.L. 1980. Arrival and departure times of Palearctic waders on the Kenya coast. *Scopus* **4**: 84-88.

PIENKOWSKI, M.W. 1979. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. *Verh. orn. Ges. Bayern* **23**: 105-124.

PIENKOWSKI, M.W. 1981. How foraging plovers cope with environmental effects on invertebrate behaviour and availability. *In* Jones, N.V. & Wolff, W.J. (eds). *Feeding and Survival Strategies of Estuarine Organisms*: 179-192. New York: Plenum Press.

PIENKOWSKI, M.W. 1982. Diet and energy intake of Grey and Ringed Plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *J. Zool., Lond.* **197**: 511-549.

PIENKOWSKI, M.W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Anim. Behav.* **31**: 244-264.

PIENKOWSKI, M.W. & EVANS, P.R. 1984. Migratory behaviour of shorebirds in the western Palearctic. *In*: Burger, J. & Olla, B.L. (eds). *Behaviour of marine animals Vol. 6. Shorebirds: migration and foraging behaviour.* New York: Plenum Press.

PIENKOWSKI, M.W. & EVANS, P.R. 1985. The role of migration in the population dynamics of birds. *In*: Sibly, R.M. & Smith, R.H. (eds). *Behavioural ecology. Ecological consequences of adaptive behaviour.* Oxford: Blackwell Scientific Publications.

PIENKOWSKI, M.W., EVANS, P.R. & TOWNSHEND, D.J. 1985. Leap-frog amd other migration patterns of waders: a critique of the Alersam and Hogstedt hypothesis, and some alternatives. *Ornis Scand.* **16**: 61-70.

PIERSMA, T. 1982. Foraging of Grey Plovers. *In*: Altenburg, W., Engelmoer, M., Mes, R. & Piersma, T. (eds). *Wintering waders on the Banc d'Arguin, Mauritania.* Report of the Netherlands Ornithological Mauritanian Expedition, 1980.

PIERSMA, T. 1985. *Wader studies and waterbirds in the Nadkong estuary, South Korea, in September 1984.* WIWO report no. 7, Zeist, Netherlands. 85 pp.

PIERSMA, T. 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. *Mar. Ecol. Prog. Ser.* **38**: 187-196.

PIERSMA, T., KLAASSEN, M., BRUGGEMANN, J.H., BLOMERT, A.-M., GUEYE, A., NTIAMOA-BAIDU, Y., VAN BREDERODE, N.E. 1990. Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. *Ardea* **78**: 123-134.

PIERSMA, T. & ZEGERS, P. 1983. Aspects of the foraging behaviour of Grey Plovers. *In*: Kersten, M., Piersma, T., Smit, C. & Zegers, P. *Wader migration along the Atlantic coast of Morocco, March 1981.* Report of the Netherlands Morocco Expedition, 1981.

PRATER, A.J. 1972. The ecology of Morecambe Bay. III. The food and feeding habits of Knot (*Calidris canutus* L.) in Morecambe Bay. *J. Appl. Ecol.* **9**: 179-194.

PRATER, A.J. 1981. *Estuary birds of Britain and Ireland.* Calton: Poyser. 440pp.

PROKOSCH, P. 1984. The German Wadden Sea. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter.* Cambridge: Cambridge University Press.

PULLIAM, H.R. 1974. On the theory of optimal diets. *Am. Nat.* **108**: 59-74.

PUTTICK, G.M. 1979. *The feeding ecology of Curlew Sandpipers* Calidris ferruginea *in the south-western Cape, South Africa.* Ph.D. thesis, University of Cape Town.

PUTTICK, G.M. 1980. Energy budgets of Curlew Sandpipers at Langebaan Lagoon, South Africa. *Estuar. Coast. Mar. Sci.* **11**: 207-215.

PUTTICK, G.M. 1981. Sex-related differences in foraging behaviour of Curlew Sandpipers. *Ornis Scand.* **12**: 13-17.

PYKE, G.H. 1979. The economics of territory size and time budget in the golden-winged sunbird. *Am. Nat.* **114**: 131-145.

RECHER, H.F. & RECHER, J.A. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. *Wilson Bull.* **81**: 140-154.

ROBERT, M. & MCNEIL, R. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* **131**: 69-79.

ROBERT, M. MCNEIL, R. & LEDUC, A. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. *Auk* **106**: 94-101.

RYAN, P.G., UNDERHILL, L.G., COOPER, J. & WALTNER, M. 1988. Waders (Charadrii) and other waterbirds on the coast, adjacent wetlands and offshore islands of the southwestern Cape Province, South Africa. *Bontebok* **6**: 1-19.

SALOMONSEN, F. 1955. The evolutionary significance of bird migration. *Dan. Biol. Medd.* **22**: 1-62.

SALOMONSEN, M.G. & BALD, R.P. 1977. Winter territoriality of Townshend's Solitaires (*Myadestes townsendi*) in a Pinon-Juniper-Ponderosa Pine ecotone. *Condor* **79**: 148-161.

SCHRAMM, M. 1978. *The feeding ecology of Grey Plover on the Swartkops estuary.* BSc.(Hons) thesis, University of Port Elizabeth.

SCOTT, D.A. 1980. *A preliminary inventory of wetlands of international importance for waterfowl in west Europe and northwest Africa.* IWRB special publication no. 2.

SEASTEDT. T.R. & MACLEAN, S.F., JR. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. *Auk* **96**: 131-142.

SELMAN, J. & GOSS-CUSTARD, J.D. 1988. Interference between foraging Redshank *Tringa totanus*. *Anim. Behav.* **36**: 1542-1544.

SENNER, S.E. & HOWE, M.A. 1984. Conservation of Nearctic shorebirds. *In*: Burger, J. & Olla, B.L. (eds). *Shorebirds: breeding behaviour and populations*: 379-421. New York: Plenum Press.

SLAGSVOLD, T. 1982. Spring predictability and bird migration and breeding times: a comment on the phenomenon of leap-frog migration. *Ornis Scand.* **13**: 145-148.

SMIT, C.J. 1981. The importance of the Wadden Sea for estuarine birds. *In*: Smit, C.J. & Wolff, W.J. (eds). *Birds of the Wadden Sea.* Rotterdam: A.A. Balkema.

SMIT, C.J. & PIERSMA, T. 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In: H. Boyd & J-Y. Pirot (eds.) *Flyways and reserve networks for waterbirds*: 24-63. IWRB Spec. Publ.

9, Slimbridge.

SMITH, P.H. & GREENHALGH, M.E. 1977. A four-year census of wading birds on the Ribble Estuary, Lancashire/Merseyside. *Bird Study* **24**: 243-258.

SMITH, A.T. & IVINS. 1986. Territorial intrusions by pikas (*Ochotona princeps*) as a function of occupant activity. *Anim. Behav.* **34**: 392-397.

SMITH, P.C. & EVANS P.R. 1973. Studies of shorebirds at Lindisfarne, Northumberland. I. Feeding ecology and behaviour of the Bar-tailed Godwit. *Wildfowl* **24**: 135-139.

SPENCER, K.G. 1953. *The Lapwing in Britain.* London: A. Brown & Sons.

STAWARCZYK, T. 1984. Aggression and its suppression in mixed species wader flocks. *Ornis Scand.* **15**: 23-37.

STENZYL, L.E., HUBER, H.R. & PAGE, G.W. 1976. Feeding behaviour and diet of Longbilled Curlew and Willet. *Wilson Bull.* **88**: 314-332.

STINSON, C.H. 1977. The spatial distribution of wintering black-bellied plovers. *Wilson Bull.* **89**: 470-472.

STINSON, C.H. 1980. Flocking and predator avoidance: models of flocking and observations on the spatial dipersion of foraging winter shorebirds (Charadrii). *Oikos* **34**: 35-43.

SULLIVAN, K.A. 1986. Influence of prey distribution on aggression in Ruddy Turnstones. *Condor* **88**: 376-378.

SUTHERLAND, W.J. 1982a. Do Oystercatchers select the most profitable cockles? *Anim. Behav.* **30**: 857-861.

SUTHERLAND, W.J. 1982b. Spatial variation in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. *J. Anim. Ecol.* **51**: 491-500.

SUMMERS, R.N. 1980. Impressions on a tropical mudflat. *Wader Study Group Bull.* **30**: 16.

SUMMERS, R.N. & UNDERHILL, L.G. 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr peninsula. *Bird Study* **34**: 161-171.

SUMMERS, R.N., UNDERHILL, L.G, PEARSON, D.J. & SCOTT, D.A. 1987. Wader migration systems in southern and eastern Africa and western Asia. *Wader Study Group Bull.* **49**, Suppl./IWRB Special Publ. **7**: 15-34.

SUMMERS, R.N. & WALTNER, M. 1979. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. *Ostrich* **50**: 21-37.

SWARTH, H.S. 1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. *University of California Publications in Zoology* **21**: 75-224.

SWENNEN, C. 1990. Oystercatchers feeding on Giant Bloody Cockles on the Banc d'Arguin, Mauritania. *Ardea* **78**: 53-62.

TERRILL, S.B. 1990. Food availability, migratory behaviour, and population dynamics of terrestrial birds during the nonreproductive season. *In*: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. (eds). *Avian foraging: theory, methodology, and applications.* Studies in avian biology 13. Cooper Ornithological Society.

TOWNSHEND, D.J. 1979. The use of space by individual Grey Plovers *Pluvialis squatarola* and Curlews *Numenius arquata* on their winter feeding grounds. *W.S.G. Bull.* **26**: 29.

TOWNSHEND, D.J. 1982. *The use of intertidal habitats by shorebird populations, with special reference to Grey Plover and Curlew.* Ph.D. thesis. University of Durham.

TOWNSHEND, D.J. 1984. The effects of predation upon shorebird populations in the non-breeding season. *Wader Study Group Bull.* **40**: 51-54.

TOWNSHEND, D.J. 1985. Decisions for a lifetime: establishment of spatial defence and movement patterns by juvenile Grey Plovers (*Pluvialis squatarola*). *J. Anim. Ecol.* **54**: 267-274.

TOWNSHEND, D.J., DUGAN, P.J. & PIENKOWSKI, M.W. 1984. The unsociable plover - use of intertidal areas by Grey Plovers. In: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter*: 140-159. Cambridge: Cambridge University Press.

TREE, A.J. 1978. Biology of the Greenshank in southern Africa. *Ostrich* **50**: 240-251.

TUBBS, C.R. 1991. The population history of Grey Plovers *Pluvialis squatarola* in the Solent, Southern England. *Wader Study Group Bull.* **61**: 15-21.

TUBBS, C.R. & WISEMAN, E.J. 1992. Severe weather wader kill in the Solent, southern England during February 1991. *Wader Study Group Bull.* **66**: 61-62.

TYE, A. & TYE, J. 1987. The importance of Sierra Leone for wintering waders. *Wader Study Group Bull.* **49**: Suppl./IWRB Spec. Publ. **7**: 71-75.

UNDERHILL, L.G. 1987. Waders (Charadrii) and other waterbirds at Langebaan Lagoon, South Africa, 1975-1986. *Ostrich* **58**: 145-155.

UNDERHILL, L.G. & COOPER, J. 1984. *Counts of waterbirds at coastal wetlands in southern Africa, 1976-1984.* Report of the Western Cape Wader Study Group and the Percy FitzPatrick Institute of African Ornithology. Cape Town: University of Cape Town.

UNDERHILL, L.G., COOPER, J. & WALTNER, M. 1980. *The status of waders (Charadrii) and other birds in the coastal regions of the southern and eastern Cape, summer 1978/79.* Cape Town: Western Cape Wader Study Group.

VAN DIJK, A.J., VAN DIJK, K., DIJKSEN, L.J., VAN SPANJE, T.M. & WYMENGA, E. 1986. *Wintering waders and waterfowl in the Gulf of Gabes, Tunisia, January-March 1984.* WIWO report no. 11.

VELASQUEZ, C.R. & HOCKEY, P.A.R. 1992. The importance of supratidal foraging habitats for waders at a south temperate estuary. *Ardea* **80**: 243-253.

VELASQUEZ, C.R., KALEJTA, B. & HOCKEY, P.A.R. 1991. Seasonal abundance, habitat selection and energy consumption of waterbirds at the Berg River estuary, South Africa. *Ostrich.*

VELASQUEZ, C.R. & NAVARRO, R. 1993. The influence of water depth on the foraging behavior of Whimbrels. *J. Field Ornithol.* **64**: 149-157.

VILALTA, A.M. 1985. Wintering waders in the Ebro Delta. *Wader Study Group Bull.* **43**: 25-28.

VINES, G. 1980. Spatial consequences of aggressive behaviour in flocks of Oystercatchers, *Haematopus ostralegus* L. *Anim. Behav.* **28**: 1175-1183.

VON HAARTMAN, L. 1968. The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fennica* **45**: 1-7.

WARWICK, R.M., GOSS-CUSTARD, J.D., KIRBY, R., GEORGE, C.L. POPE, N.D. & ROWDEN, A.A. 1991. Static and dynamic enviroment factors determining the community structure of estuarine macrobenthos in S.W. Britain: why is the Severn estuary different? *J. Appl. Ecol.* **28**: 329-345.

WERNSTEDT, F.L. 1972. *World climatic data.* Lemont: Climatic Data Press.

WHITELAW, D.A., UNDERHILL, L.G., COOPER, J. & CLINNING, C.F. 1978. Waders (Charadrii) and other birds on the Namib Coast: counts and conservation priorities. *Madoqua* **2**: 137-150.

WHITFIELD, D.P. 1985. Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**: 544-558.

WHITFIELD, D.P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus*. *Ibis* **130**: 284-287.

WIENS, J.A. & ROTENBERRY, J.T. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.* **51**: 21-41.

WILLIS, E.O. 1972. Do birds flock in Hawaii, a land without predators. *Calif. Birds* **3**: 1-8.

WOLFF, W.J. 1969. Distribution of nonbreeding waders in an estuarine area in relation to the distribution of their food organisms. *Ardea* **57**: 1-28

WOLFF, W.J. & SMIT, C.J. 1984. The Dutch Wadden Sea. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter.* Cambridge: Cambridge University Press.

WOOD, A.G. 1984. *Time and energy budgets of the Grey Plover* (Pluvialis squatarola) *at Teesmouth*. Ph.D. thesis, University of Durham.

WOOD, A.G. 1986. Diurnal and nocturnal territoriality in the Grey Plover at Teesmouth, as revealed by radio telemetry. *J. Field Ornithol.* **57**: 213-221.

YATES, M.G., GOSS-CUSTARD, J.D., MCGRORTY, S., LAKHANI, K.H., DIT DURELL, S.E.A. LE V., CLARKE, R.T., RISPIN, W.E., MOY, I., YATES, T., PLANT, R.A. & FROST, A.J. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J. Appl. Ecol.* **30**: 599-614.

ZWARTS, L. 1978. Intra- and inter-specific competition for space in estuarine bird species in a one-prey situation. *Int. Orn. Congr.* **17**: 1045-1050.

ZWARTS, L. 1981. Habitat selection and competition in wading birds. *In*: C.J. Smit & W.J. Wolff (eds). *Birds of the Wadden Sea*. Rotterdam: A.A. Balkema.

ZWARTS, L. 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. Ardea 73: 3-12.

ZWARTS, L. 1988. Numbers and distribution of coastal waders in Guinea-Bissau. *Ardea* **76**: 42-55.

ZWARTS, L. 1990. Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. *Ardea* **78**: 279-300.

ZWARTS, L. & BLOMERT, A-M. 1990. Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. *Ardea* **78**: 193-208.

ZWARTS, L., BLOMERT, A-M., ENS, B.J., HUPKES, R. & VAN SPANJE, T.M. 1990a. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania? *Ardea* **78**: 39-52.

ZWARTS, L., BLOMERT, A-M. & HUPKES, R. 1990b. Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* **78**: 237-256.

ZWARTS, L. & DIRKSEN, S. 1989. Feeding behaviour of Whimbrel and anti-predator behaviour of its main prey, the fiddler crab *Uca tangeri*. *In*: Ens, B.J., Piersma, T., Wolff, W.J. & Zwarts, L. 1989 (eds.). *Report of the Dutch-Mauritanian project, Banc d'Arguin 1985-86*, pp. 205-207.

ZWARTS, L. & DIRKSEN, S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* **78**: 257-278.

ZWARTS, L. & DRENT, R.H. 1981. Prey depletion and the regulation of predator density: Oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). *In* Jones, N.V. & Wolff, W.J. (eds). *Feeding and Survival Strategies of Estuarine Organisms*: 193-216. New York: Plenum Press.

ZWARTS, L., ENS, B.J., KERSTEN, M. & PIERSMA, T. 1990c. Moult, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* **78**: 339-364.

ZWARTS, L. & ESSELINK, P. 1989. Versatility of male Curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability. *Mar. Ecol. Prog. Ser.* **56**: 255-269.

ZWARTS, L., FELEMBAN, H. & PRICE, A.R.G. 1991. Wader counts along the Saudi Arabian coast suggests the Gulf harbours millions of waders. *Wader Study Group Bull.* **63**: 25-32.

ZWARTS, L. & WANINK, J. 1984. How Oystercatchers and Curlews successively deplete clams. *In*: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds). *Coastal waders and wildfowl in winter*: 69-83. Cambridge: Cambridge University Press.